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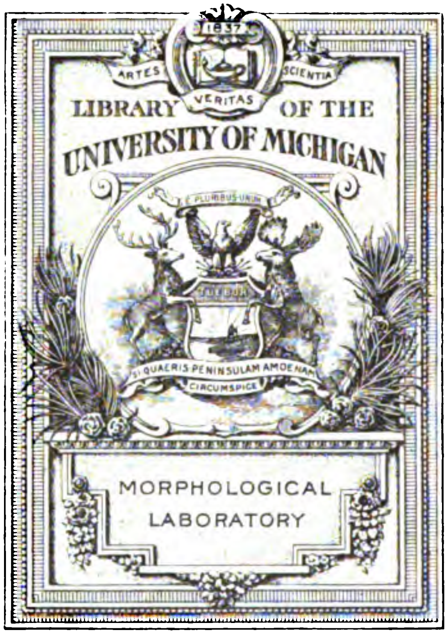

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OF THE
LELAND STANFORD JUNIOR UNIVERSITY

XVIII

THE
Phosphorescent Organs in the Toadfish Porichthys Notatus Girard

BY

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PREFATORY NOTE.

This memoir is the eighteenth of a series expressing the results of the investigations and explorations connected with the Hopkins Seaside Laboratory, an adjunct of the biological laboratories of the Leland Stanford Junior University. These investigations have been carried on by means of the assistance given by Timothy Hopkins, Esq., of Menlo Park, California. This contribution appears in the JOURNAL OF MORPHOLOGY, the present edition being a reprint.

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Directors Hopkins Seaside Laboratory.

Date of publication, March 1, 1899.

THE PHOSPHORESCENT ORGANS IN THE TOAD-FISH, PORICHTHYS NOTATUS GIRARD.

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I. INTRODUCTION.

FISHES described as possessing phosphorescent organs belong almost without exception to the deep-sea fauna. They live at depths where the light of the sun rarely if ever penetrates, and this fact is supposed to account for the process of evolution which has brought about the phylogenetic development of light-producing organs. It lent interest, therefore, to the study of phosphorescent organs in fishes when in 1889 a paper appeared, describing phosphorescent organs in Porichthys, a shore fish. The study of these organs was made on unfavorable material, as the author states, and as the structures described were so obviously different from phosphorescent organs in other fishes, it seemed desirable to reinvestigate the question.

It is my purpose in this paper to present the distribution, structure, and development of the phosphorescent organs in Porichthys, together with their surface relations to the lateral-line system of sense organs.[1] In the future I hope to follow with a second paper on the morphology of the lateral-line system, work now partially completed.

The results presented in this paper were obtained chiefly from the study of Porichthys notatus Girard. But I have also some material from Porichthys nautopedium Jordan and a new species of Porichthys kindly furnished me by Prof. C. H. Gilbert.

Porichthys notatus is found abundantly along the Pacific coast from Sitka to Panama. It is taken in early spring and summer at tide water where it comes to spawn. The eggs are cemented in a single layer to the under surfaces of stones, and, as the male remains with the brood until the young become free-swimming (when they are about one inch in length), it is comparatively easy to secure adults together with young. Adults are also taken in large numbers in the trawls on the fishing banks north of San Francisco in spring and summer. In winter they are very scarce on the banks.

In a surface view, the phosphorescent organs appear as bright silvery spots distributed in lines or rows over the surface of the body of the fish. The average number of organs is about 350 on each side of the fish, 700 organs in all. Of these, 275 on either side are located in eight lines on the ventral and ventro-lateral surface of the body. In this region the rows are very conspicuous (Pl. XXXVIII, Figs. 1 and 2), but more obscure or sometimes entirely absent over the dorsal aspect of the body. Each organ, viewed from the surface, appears as a silvery spot more or less circular in outline and varying in size from a point scarcely visible with the unaided eye to .8 mm. in diameter. The larger organs are found on the ventral surface of the fish, the less conspicuous ones on the dorsal surface — a fact to be again referred to later in the paper. They are often surrounded by, or bordered on one side by, an increased amount of pigment. This is especially noticeable in organs on the sides of the body where the pigment is much increased in amount on the side of the organ away from the mid-ventral line.

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[1] The material for this study was collected and the work begun at the Hopkins Seaside Laboratory, Pacific Grove, Cal., in the summers of 1892 and 1894. I am deeply indebted to the directors, Dr. O. P. Jenkins and Dr. C. H. Gilbert, for the privileges of the laboratory and for advice and encouragement. I wish also to express my indebtedness to Dr. C. O. Whitman for the privileges of a table at the Marine Biological Station, Woods Holl, Mass., during the summers of 1896 and 1897; also to thank the members of the instructing corps for suggestive criticism and advice. Miss Clapp has kindly allowed me to examine her manuscript on the Lateral-Line System of Opsanus tau, and has criticised my manuscript, as well as given me many suggestions as to methods of making preparations. And, finally, I am especially indebted to my wife, whose invaluable criticism and enthusiastic interest have been my constant support.

The structures, indiscriminately designated by Test as "lateral-line organs," "slime glands," "mucous pores," or "pores," are in reality lateral-line sense organs of the kind designated as nerve hillocks by Merkel. Such an organ, viewed from the surface, presents a point on the epidermis free from pigment, the end of the sense organ itself with its immediately surrounding supporting cells. It is too distinct and characteristic in appearance to be mistaken by even the most casual observation.

The lines of phosphorescent organs and lateral-line organs are so closely associated in their distribution in the skin of the fish that they may be most economically mapped out together. Test did not discriminate between these two sets of organs. Terms he introduced, referring to lines of organs, will be indicated by quotation.

II. DISTRIBUTION OF THE PHOSPHORESCENT ORGANS AND THE LATERAL–LINE SENSE ORGANS.

The organs of both systems are arranged in lines or rows and are very constant in their relation to each other in any given row, also the rows are constant in their relative positions in different individual fishes. The number of organs in a given line of either phosphorescent organs or sense organs may, however, vary much in different individuals (see Table). The average number only will in most instances be given in the general description.

The lateral-line organs are located free on the surface with the exception of certain rows on the head which are in canals. These lines of canal organs form only a small part of the lateral-line system in Porichthys. Unless otherwise specified, surface organs are meant.

It is impossible to determine the homologies of the parts of the complex lateral-line system without a knowledge of the development of the sensory Anlage and of the innervation of the system, including the origin of the nerves in the central nervous system. Such a study has been made in part for only a few fishes, while the great mass of fishes remain unknown in this regard. It is necessary, therefore, while awaiting the development of our knowledge of the origin and distribution of the lateral-line nerves, to designate the groups of lateral-line organs in particular species by some sort of descriptive terms. The intention in this paper is not so much to name the groups in Porichthys as to describe their location by short descriptive terms that will serve temporarily, *i.e.*, until we have a surer foundation for establishing homologies between the parts of the lateral-line system in different species of fishes, when a permanent nomenclature may be adopted.

1. *Lines of Organs on the Body.*

The lateral row, *la* (Pl. XXXVIII, Figs. 1–3), begins on the side at a point posterior to the upper border of the pectoral fin and directly below the third dorsal ray. It runs straight back along the side to the upper third of the base of the caudal, and contains both kinds of organs. This line contains an average of thirty-six sense organs with a phosphorescent organ immediately below and generally one above each sense organ. In the lower series the phosphorescent organs are well developed and large, but the organs of the upper series are quite small and rudimentary; in fact they are often wanting, there being only an average of twenty-two in the fifteen specimens tabulated. The organs in this line correspond very nearly with the segments of the part of the body along which they lie. They are found above the grooves which mark the boundary between the myomeres.

The "pleural" row, *pl*, consists of parallel lines of phosphorescent organs and sense organs. The row of phosphorescent organs begins at a point posterior to the middle of the base of the pectoral and below the anterior ray of the dorsal fin. The line curves backward and downward to a point back of the lower edge of the pectoral and above the first anal ray, thence straight back along the side, ending usually above the twenty-third anal ray. The organs of this line vary in number from forty-three to sixty-two, or an average of fifty-three, and have no relation to the body segments. The row of sense organs is located immediately below the row of phosphorescent organs and follows the same general course. This row usually extends backward only to the thirteenth anal ray, but in three specimens from Alaska (see Table, Nos. 8–10) the row extends to the base of the caudal fin. There is an average of thirty-two sense organs in the row, excluding the three exceptions mentioned. In these three there are sixty, bringing the general average up to thirty-six.

There are two caudal, *ca*, lines of sense organs on each side the fin, located on the upper and lower thirds, respectively. These rows contain only sense organs, which are well developed at the base of the caudal, but become smaller toward the extremity of the fin. There are as many as twenty-five in each line in the oldest specimens, but the number varies greatly, increasing with the age of the specimen. These rows are in line with the lateral and pleural rows of sense organs, but they are not continuous with them.

The "anal" row, *a*, runs along the body on either side of the base of the anal fin from opposite the interspace between the second and third anal rays to the base of the caudal. The phosphorescent organs of this line correspond in position to the anal rays and are in pairs, with exceptions to be mentioned. The first organ is usually single; the next twenty-eight or twenty-nine, paired; the last six or seven, single. The last four or five organs are situated under the base of the caudal and are arranged in a markedly compact row. There is an average of thirty-six organs in this row, counting the pairs but once. The outer organs of the pairs are apparently larger than the inner, but this appearance is in part due to the fact that the inner organs are more deeply buried in the angle of the base of the fin. The posterior two or three pairs are closely united. The anal row contains a single line of sense organs. There are thirty-four of these organs in the line. The first is placed just in front of the second pair of phosphorescent organs, and each successive one bears the same relation to its corresponding phosphorescent organ, except the last two, which are placed external to and just above the four or five phosphorescent organs along the base of the caudal.

The "ventral rows, *v*, form a parenthesis on the stomach," extending from the side of the anus three-fourths the distance to the ventral fin. The anterior ends of the two rows are usually continuous with each other, and comprise thirty-four phosphorescent organs on either side. The organs present a clear, circular outline without apparent increase of pigment around them. These rows are not accompanied by sense organs.

The "gastric" line of phosphorescent organs, *ga*, begins a little below the middle of the front of the base of the pectoral, curves forward, downward, then backward, around the lower edge of the pectoral; then extends straight back along the side of the belly to a point dorsal to the anterior edge of the anal papilla. The line contains an average of thirty organs, about ten in the curved portion and twenty in the straight part of the line.

The "gular" line, *gu*, begins a little back of the isthmus and runs parallel with its fellow backward to the posterior and ventral side of the ventral fin, then curves outward and backward to a point below the anterior end of the straight portion of the gastric line. There is an average of twenty-seven organs in this row. The gular line gives off a short spur of seven organs running forward along the external border of the ventral fin.

The gastro-gular line, *ga gu*, of sense organs begins at the isthmus somewhat anterior to the end and toward the median ventral side of the phosphorescent row, runs posteriorly parallel to the phosphorescent line to its end, then backward parallel to the gastric row, curves upward around its posterior end, and terminates in close relation to the pleural row of sense organs (see Pl. XXXVIII, Fig. 1). There are fifty organs in the entire row.

The "scapular" row, *sc*, begins just back of the posterior pore of the temporal canal, runs straight back above the pectoral fin, then curves in toward the base of the dorsal fin, where it is continued into the dorsal row at the base of the third dorsal ray. There are seventeen sense organs in this row, with an average of ten phosphorescent organs alternating with them.

The straight part of the scapular row is accompanied by a scapular accessory row, *sc ac*, of three to five sense organs, with a small phosphorescent organ above each.

The dorsal row, *d*, extends along the dorsal surface of the body at the base of the dorsal fin from the third dorsal ray to the caudal peduncle. This row contains an average of seventy-one sense organs. Rarely phosphorescent organs are found between the first three or four organs of the row, but in such exceptional specimens they are always small and rudimentary.

Outside the dorsal row is an irregular line, or accessory row, *d ac*, which contains sense organs and rudimentary phosphorescent organs arranged as in the lateral line. The number of organs in this row is quite variable, an average of sixteen in five specimens (see Table).

2. *Organs of the Lower Jaw and Head.*

The branchiostegal row, *br*, begins in front of the isthmus and extends outward over the membrane of the gill-cover to the base of the lower branchiostegal ray; then along the membrane between the first and second rays almost to the edge of the gill-cover. There are thirty-four phosphorescent organs in this line and no sense organs.

The "mandibular" row, *md*, of phosphorescent organs extends around the inner rim of the ridge formed by the dentary bones. It contains twenty-two organs on either side.

The operculo-mandibular row consists of surface organs and canal organs. It begins on the side of the head at the anterior pore of the temporal canal. It runs downward on the surface to in front of the opercular spine, where it sinks into a canal. This canal extends along the posterior border of the preopercle, around the angle of the mouth, and forward on the ventral surface of the mandible to near its anterior end, where the line comes again to the surface and ends at the symphysis of the jaw (Pl. XXXVIII, Fig. 2). There are eight pores or openings to the canal portion. This line contains twenty-one organs, seven at the upper free end, seven in the canal, and seven at the lower free end. At the upper free end there are occasionally rudimentary phosphorescent organs between the sense organs — an average of one.

There are two "opercular" rows, an upper and a lower. The upper row, *u op*, contains ten phosphorescent organs and fourteen sense organs. These are arranged in parallel lines, the phosphorescent organs above and the sense organs immediately below them. The line begins posterior to the second pore from above of the operculo-mandibular canal, and extends in a curve backward and upward, over the operculum, to a point posterior to the opercular spine. The row of sense organs is the longer of the two.

The lower row, *l op*, contains from two to ten phosphorescent organs, on an average four, and an average of seventeen sense organs, the phosphorescent organs occurring between the sense organs at the base of the line. The row begins opposite the third operculo-mandibular pore and extends backward and upward to near the posterior angle of the opercular flap. The curvature of the lower row is a little greater than that of the upper, the two ending near each other.

The infraorbital consists of two portions, a preorbital and a suborbital, each of sense organs. The preorbital or nasal portion is made up of a row of four to six organs from the posterior nasal opening to the base of the anterior nasal papilla, two pairs of organs between the anterior nasal papillae, and two to three more in a transverse line at the posterior base of the tube. The suborbital extends from the posterior nasal opening around under the eye to the anterior pore of the temporal canal. It contains fourteen sense organs and one large phosphorescent organ below the posterior border of the eye.

The temporal canal (Pl. XXXVIII, Fig. 3, *t*) corresponds to the squamosal of Allis in Amia. It contains a single canal organ. Above this canal are two free organs. The infraorbital, temporal, scapular, and dorsal form a continuous series of sense organs.

A short maxillary canal, *mx*, with two organs, extends along the maxillary bone below the posterior nasal opening. At its lower end are two free organs with a small phosphorescent organ above each in very old specimens.

A malar row of sense organs, *ma*, extends downward from the suborbital across the cheek to the angle of the mouth, thence along the mandible over the operculo-mandibular canal to its anterior end. There are thirty-one organs in this row, thirteen in the malar portion and eighteen in the mandibular. Two spurs are connected with this line, a short anterior spur of two organs from the middle of the cheek portion of the line and a second posterior one of four to five organs from the angle formed at the mouth.

The supraorbital line, *sup o*, is enclosed in a canal which begins by a pore at the median border of the posterior nasal opening, runs backward and inward toward the median line of the head, where it anastomoses with its fellow of the opposite side at a point in a transverse line drawn through the posterior border of the lens of the eye. Here the canals diverge and each runs to a point behind the eye a distance equal to half the diameter of the latter. This canal opens at its ends only. Five sense organs are found in the canal — three in the anterior part and two in the posterior limb.

The "frontal" group, *fr*, consists of two rows of organs. It is located over the posterior end of the frontal bone, about midway from the median line of the head to the outer edge of its flat top. The outer row of each group consists of an average of six sense organs, with five phosphorescent organs, alternating in a longitudinal row. The inner row is a shorter one, parallel with the posterior part of the outer row, and consists of from four to five sense organs with phosphorescent organs at the inner and outer edge of each sense organ. The phosphorescent organs of this group, like those of other dorsal groups, are especially variable in number and rudimentary.

The "occipital" row, *oc*, contains from nine to twelve sense organs, sometimes with a pair of rudimentary phosphorescent organs on the inner and outer side of each sense organ, sometimes with no phosphorescent organs. The row begins near the posterior edge of the spinous dorsal, curves first inward toward the median dorsal line, then outward and forward (see Pl. XXXVIII, Fig. 1).

In a species described from the Galapagos Islands, Porichthys nautopedium Jordan, the arrangement of phosphorescent organs and sense organs corresponds, group for group, with that given above. There are only slight variations from the average number of organs, except in the pleural row, which, like the pleural row of three specimens from Alaska (Table, Nos. 8–10), is continued back to the base of the caudal.

In the new species of Porichthys previously referred to, obtained recently at Panama by Dr. Gilbert, the location of the lines of phosphorescent organs and sense organs corresponds very closely with that in Porichthys notatus. Also the number of both kinds of organs, as will be seen by a reference to the appended table, Nos. 16 and 17, is very similar to the number in the common form. It may be noted, however, that on the dorsal surface, where in Porichthys notatus rudimentary organs are found, phosphorescent organs are wholly absent. The phosphorescent organs on the ventral surface of this species are not more than half as large as in the common species.

In general, we may say that the phosphorescent organs of the three species of Porichthys studied are always well developed and prominent along the ventral and ventro-lateral surfaces of the body, while along the dorsal surface they are markedly small and rudimentary, and are very variable in their development in the different specimens of the same species.

The sense organs, on the other hand, are quite constant both in their presence and the extent of their development in the different regions. The sense organs are accompanied by dermal papillae, two for each organ. These dermal papillae differ very much in the extent of their development, being most southern Alaska coast. Specimens 16 and 17,

Temporal. S.O.	Maxillary. S.O.		Malar.		Supraorbital. S.O.	Outer Frontal.		Inner Frontal.			Occipital.		
			Ph.	S.O.		Ph.	S.O.	Ph.	S.O.	Ph.	Ph.	S.O.	Ph.
1	2+	—	—	—	—	5	5	5	5	5	4	9	4
1	2+	—	—	27	—	7	9	3	5	—	0	10	—
1	2+	—	—	—	—	6	7	3	5	2	4	9	4
1	2+	—	4	33	—	5	6	—	4	2	1	9	3
1	2+	—	—	29	—	5	6	1	4	4	0	10	—
1	2+	—	—	25	—	5	6	1	3	1	3	11	1
1	2+	—	4	26	—	5	5	4	4	—	2	8	3
1	2+	—	—	—	—	7	7	5	5	3	12	12	12
1	2+	—	—	—	—	7	7	—	3	—	—	9	—
1	2+	—	—	—	—	6	6	5	7	5	—	12	—
1	2+	—	4	35	—	4	7	4	4	4	—	9	—
1	2+	—	0	34	—	—	—	—	—	—	0	9	0
1	2+	2	2	35	5	6	6	5	5	5	0	8	0
1	2+	2	5	25	5	0	6	2	4	2	0	10	0
1	2+	2	0	37	5	7	7	3	5	3	0	12	4
1	2+	2	3	31	5	5	6	3	4	2	2	10	2
1	—	—	0— 5	25— 37	5	0— 7	5— 9	0— 5	3— 7	0— 5	0— 12	8— 12	0— 12
1	—	—	—	—	—	0	10	0	5	0	—	—	—
1	—	—	0	25	—	0	8	0	7	0	0	11	0

marked in the nasal, dorsal, anal, and mandibular lines. In these lines they often reach a length of 2 mm., and are three and four parted at their ends.

III. Structure of the Phosphorescent Organs.

Organs from different parts of the body have a common general structure, differing only in minor details. It will, therefore, be sufficient to describe a typical organ in detail and later compare with it those organs which have a specialized form or structure.

The epidermis of Porichthys has no scales and is richly supplied with large, club-shaped mucous cells in all stages of development. The dermis is quite a thick layer of dense connective tissue bearing blood vessels, nerves, and pigment cells. The phosphorescent organs are imbedded in the deeper portion of this dermis.

Each organ consists of four parts (Pl. XXXVIII, Fig. 4, and Pl. XXXIX,^{a} Figs. 5 and 9), the lens, the gland, the reflector, and pigment.

1. *The Lens.*

In a typical organ, from the anal or ventral row, for example, the outer or more superficial portion of the organ consists of a group of cells, the lens (Pl. XXXIX,^{a} Fig. 5, *l*). The surface of the lens directed toward the exterior, the distal portion, is oval or spherical in outline, while the deeper or proximal portion is projected into a more or less pronounced subconical form. The cells of the lens are polygonal in form in the center of the structure, becoming flattened toward the surface. At the distal surface the cells are quite regular and form a pavement-like layer (Pl. XXXIX,^{a} Figs. 5 and 9), but in the deeper conical portion the cells are very irregular in form, often with processes which interlace in a confused mass at the extreme proximal part. The lens cells have a small oval nucleus which is very sharply defined in contrast with the modified cytoplasm. The cell body is very dense, homogeneous, and highly refractive. The coagulation of this dense substance by reagents often slightly separates the cells, thus rendering their outlines in sections very distinct.

The lens has no capillaries distributed to its substance. In Golgi preparations nerve fibers were found distributed to the superficial part of the lens and terminating among its cells in small free varicose ends. The number was, however, not greater than that found in the surrounding connective tissue of the skin and seems, therefore, of no special significance (Pl. XXXIX,[a] Fig. 8).

2. *The Gland.*

The gland forms a shallow cup surrounding the proximal two-thirds of the lens. It is composed of cells varying greatly in size and shape (Pl. XXXIX,[a] Figs. 5–7). The gland cells are held in a mesh of connective tissue and capillaries and in part by processes from the cells of the base of the lens. They have their long diameters placed vertical to that portion of the surface of the lens along which they lie. These cells have large round nuclei which are often vacuolated. The cytoplasm of the cells is very granular and is stained with the greatest difficulty. In alcoholic material these gland cells present an appearance which indicates that their granular constituents are largely dissolved out. In fact it is impossible to gain a true idea of the character of these cells from such material, as I found after many trials. On the other hand, the cells are beautifully preserved in Flemming's fluid and present in such preparations the structure shown in Pl. XXXIX,[a] Figs. 6 and 7.

The gland is richly supplied with blood vessels, which enter around the distal border and also by puncturing the reflector below. The capillaries form a network among the gland cells and are in sections generally filled with red and white corpuscles.

3. *The Reflector.*

The reflector forms one of the most striking structures of the organ. It also is a cup-shaped mass which encloses the gland and the proximal portion of the lens, extending up around the latter for over two-thirds of its surface (Pl. XXXVIII, Fig. 4, and Pl. XXXIX,[a] Fig. 5). The reflector is composed of connective tissue, the matrix of which is modified into peculiar fine strands or fibrils, called spicules. These spicules very strongly reflect light. This property is very manifest even in the thinnest of sections where the reflector is dark gray or brown by direct light but bright silvery by reflected light. The spicules form a dense mass of fibrils somewhat regularly parallel with the surface of the lens. Small oval nuclei are scattered throughout the reflector, also a certain number of ordinary connective-tissue fibrils are scattered among the spicules, especially toward the periphery of the cup. That these fibrils are not "calcareous spicules," as von Lendenfeld describes for phosphorescent organs of Scopelus and other deep-sea forms, is evident, since they are not altered by nitric acid, nor, in fact, by any of the numerous fixing reagents used in their preparation.

Small blood vessels are found in the reflector, but only as they pierce the structure to reach the gland within.

4. *The Pigment.*

The pigment mass is composed of the large, many-branched type of cells characteristic of the pigment cells of the skin of fishes and amphibia generally. The cells are located around the outer and deeper surface of the reflector and vary in number in different organs. They are sometimes so numerous as to form dense masses, and again, as in the ventral or anal rows, there may be only three or four such cells to the organ.

IV. NERVE SUPPLY OF THE PHOSPHORESCENT ORGANS.

A most diligent and persistent effort was made to demonstrate the presence of a special nerve supply to the phosphorescent organs. Numerous preparations of the skin containing the organs were prepared by the methods which give specific nerve staining. By the iron-haematoxylin method and by the gold-chloride method, no nerves could be distinguished in the organs. By the Golgi method beautiful preparations were obtained showing the distribution of nerves to the skin and to the epidermis, but in only two sections were nerves shown to have direct relation to the phosphorescent organ. The better one of these sections (Pl. XXXIX, Fig. 8) showed nerves branching over the surface of the lens. Whole mounts of the skin were made by the methylen-blue method of Bethe. These showed the most detailed network of nerve fibers lying in the connective tissue of the skin. Preparations containing both phosphorescent organs and lateral-line sense organs showed branches of the lateral-line nerve coming off the main stem and ending in the sense organs with almost diagrammatic regularity. Nerve fibers or bundles of nerve fibers were found in the skin above or below the phosphorescent organs, but no nerve bundles penetrated the phosphorescent organs and ended there. Two organs out of a very large number prepared contained each a single nerve fiber which entered the organ and terminated there. In one or two others single fibers seemed to terminate in the organ, but the fact could not be determined with certainty.

The facts set forth above, based on very favorable preparations, justify the conclusion that *the phosphorescent organs of Porichthys possess no specific nerve supply*. The few individual nerve fibers demonstrated to enter the organ may be considered as branches from the general nerve supply of the skin.

V. Orientation of the Organs with Reference to the Surface of the Body.

A line passing through the middle of the three parts of the phosphorescent organ may be taken as its axis, and the position of this axis with reference to the body surface as the direction or position of the organ. In the ventral rows of the body the organs are directed downward, that is, the axes of the organs are almost or quite vertical with the surface of the body of the fish. The organs on the sides of the body and the lower part of the head are directed downward and slightly outward, and the axis of each organ thus makes quite a wide angle with the vertical to the surface. In the pleural row this angle is from

30° to 40°, while in the lower series of the lateral row it is often 80° or more ; in fact the axis is sometimes quite tangent to the surface of the body at that point. In this class of organs a variation from the typical arrangement of the parts may be noted. In a transverse section of such an organ, say from the pleural row, the deeper part of the cup of the reflector extends inward and upward (Pl. XXXIX^a, Fig. 10) ; that is, toward the dorsal part of the fish. It forms a somewhat deeper pocket than is formed by organs on the ventral surface. In such specimens the pigment is amassed around the upper or dorsal portion of the reflector. In these organs on the side of the body the conical base of the lens is relatively longer and is always in the axial line of the organ. The cells of the gland in such organs are arranged radially around the conical part of the lens.

The organs on the dorsal surface of the body and head have their axes vertical to the surface of the body. All these organs are small and rudimentary and irregular in their development, as shown by the fact that the lens is small and irregular in form, that the gland and reflector have more ordinary connective tissue in their structure, and especially by the inconstancy in the presence of the dorsal organs in different individual fishes.

VI. Development of the Phosphorescent Organs.

The phosphorescent organs arise quite late in the development of the embryo. In skins of embryos 8.5 to 8.9 mm. in length, and in a transverse serial section of an embryo not measured but probably of about the same length, I find the first or incipient stages in the development of the rows of phosphorescent organs on the ventral surface of the body. The organs appear first in the ventral, gastric, branchiostegal, and apparently also in the anal rows at the same time. In the anal row it is not easy to determine their first appearance, owing to the changes accompanying the development of the fin.

In embryos 8 mm. in length the sensory Anlage of the lateral-line system is complete and the sense organs are sufficiently well differentiated to be counted in skins. But the ventral and branchiostegal rows are not accompanied by sense organs, and, therefore, furnish a crucial test as to the origin of the organs. In the serial sections of the embryo mentioned above, the basal layer of cells of the epidermis of the ventral side of the body is slightly thickened in the region occupied by the adult ventral line (Pl. XL,[a] Fig. 13). The thickening is produced by a more rapid increase in the number of the epidermal cells in the particular area.

In the gastric row of the same specimen there is a similar multiplication of cells just above the accompanying sensory Anlage (Pl. XL,[a] Fig. 14). In this case the multiplication of cells shows a sort of center toward which the surrounding nuclei perceptibly converge. This is the beginning of a cell aggregation which soon proliferates into well-marked centers or groups, the antecedents of the individual organs of the line. In this incipient stage of the gastric organs the cells lie immediately against the cells of the sensory Anlage of the gastrogular row of sense organs, but they show no other evidence of origin from it. In skins it happened in one instance that the sensory Anlage of this row was torn free of the epidermis, and the cells along its upper border were apparently undisturbed. They were slightly increased in number, however, indicating a stage comparable to that from the ventral line figured in cross-section in Pl. XL,[a] Fig. 13, or in the corresponding line in Pl. XL,[a] Fig. 14.

Although it would seem impossible to affirm that the origin of the phosphorescent organs in the gastric row is independent of the sensory Anlage which has arisen by migration of cells, yet I am convinced that such is the case. The above facts, especially the independence of the origin of the rows above mentioned not associated with sense organs, form the basis of my belief that *the phosphorescent organs arise by local proliferation of cells from the epidermis in the region which they permanently occupy.*

The further progress in the development of the phosphorescent organ consists in the rapid multiplication of cells, giving rise to a distinct nodule which projects as a small papilla from the inner surface of the epidermis (Pl. XL,^{a} Figs. 15 and 16). The orientation of the organ is determined in this very early stage. Organs of the ventral line are vertical to the surface of the skin, while organs of the ventro-lateral surfaces are oblique (Pl. XL,^{a} Figs. 15–20). In embryos 13 mm. long this papilla, in vertical section of ventral organs, presents the general outline of a finger-tip. It has a diameter of about six cells and is four to five cells deep. Pigment cells now appear in the connective tissue beneath the organ and are found in almost every section. In skins they show as the much-branched type of pigment cell spreading over the inner surface of the papilla. In specimens 14 mm. long there are from three to six such cells around each organ.

The next stage consists in the gradual separation of this papilla from the epidermis. The papilla becomes constricted where its sides are continuous with the general epidermis, the constriction continuing until complete separation occurs. At the same time a new layer of columnar cells forms in the epidermis and all evidence of the former union is obliterated. The separated mass now has a diameter of about .04 mm. and is found in embryos 18 to 20 mm. in length.

Soon after separation from the epidermis occurs, in fact before in some instances (Pl. XXXIX,^{a} Fig. 12, and Pl. XL,^{a} Fig. 21), the structure elongates slightly in the line of the axis of the developing organ and a differentiation occurs near the base, enabling one to distinguish in the mass two parts, an outer to become the lens and an inner the gland. No separation occurs between the two portions, yet the cells of each become more and more specialized in the direction of the cells of the adult lens and gland, respectively. By the time the embryo becomes free swimming, a length of about 25 mm., the organs possess the general characters of adult organs. Later growth consists in a great increase in size, due to the multiplication of the cells in the lens and gland, respectively.

Accompanying the differentiation of the lens and the gland there is a corresponding differentiation of the capsule. The connective-tissue cells of the dermis first form a cup-shaped aggregation around the base of the epidermal portion of the developing organ (Pl. XL,^{a} Figs. 21, 23, and 24). The matrix of these connective-tissue cells is gradually converted into the modified fibrils which characterize the adult reflector (Pl. XXXIX,^{a} Figs. 9–11, and Pl. XL,^{a} Fig. 24). These fibrils are at first intermixed with a large amount of ordinary connective-tissue strands but ultimately form almost the entire mass. The pigment cells likewise increase in number and form masses of cells about the reflector, especially in organs on the side of the body.

Organs in different rows do not appear at the same time. Those on the mandible and ventral surface of the body appear first, and since they reach the highest development are taken as types. The lower series of the lateral line at 20 mm. is not farther advanced than organs of the ventral line at 11 to 12 mm. Those organs above the lateral line appear later and are always very rudimentary. In fact, such organs as I have designated rudimentary are never present above the lateral line and on the dorsal surface of the body up to the time when the embryos become free-swimming, a length of at least 25 mm.

VII. FUNCTION OF THE PHOSPHORESCENT ORGANS.

I have kept specimens of Porichthys in aquaria at the Hopkins Seaside Laboratory, and have made numerous observations on them with an effort to secure ocular proof of the phosphorescence of the living active fish. The fish was observed in the dark when quiet and when violently excited, but, with a single exception, only negative results were obtained. Once a phosphorescent glow of scarcely perceptible intensity was observed when the fish was pressed against the side of the aquarium. Then, this is a shore fish and quite common, and one might suppose that so striking a phenomenon as it would present if these organs were phosphorescent in a small degree would be observed by ichthyologists in the field, or by fishermen, but diligent inquiry reveals no such evidence.

Notwithstanding the fact that Porichthys has been observed to voluntarily exhibit only the trace of phosphorescence mentioned above, still the organs which it possesses in such numbers are beyond doubt true phosphorescent organs, as the following observations will demonstrate.

A live fish put into an aquarium of seawater made alkaline with ammonia water, exhibited a most brilliant glow along the location of the well-developed organs. Not only did the lines of organs shine forth, but the individual organs themselves were distinguishable. The glow appeared after about five minutes, remained prominent for a few minutes, and then for twenty minutes gradually became weaker until it was scarcely perceptible. Rubbing the hand over the organs was followed always by a distinct increase in the phosphorescence. Pieces of the fish containing the organs taken five and six hours after the death of the animal became luminous upon treatment with ammonia water.

Electrical stimulation of the live fish was also tried with good success. The interrupted current from an induction coil was used, one electrode being fixed on the head over the brain or on the exposed spinal cord near the brain, and the other moved around on different parts of the body. No results followed relatively weak stimulation of the fish, although such currents produced violent contractions of the muscular system of the body. But when a current strong enough to be quite painful to the hands while handling the electrodes was used, then stimulation of the fish called forth a brilliant glow of light from apparently every well-developed organ in the body. All the lines on the ventral and lateral surfaces of the body glowed with a beautiful light, and continued to do so while the stimulation lasted. The single well-developed organ just back of and below the eye was especially prominent. No luminosity was observed in the region of the dorsal organs previously described as rudimentary in structure. I was also able to produce the same effect by galvanic stimulation, rapidly making and breaking the current by hand.

The light produced in Porichthys was, as near as could be determined by direct observation, a white light. When produced by electrical stimulation it did not suddenly reach its maximal intensity, but came in quite gradually and disappeared in the same way when the stimulation ceased. The light was not a strong one, only strong enough to enable one to quite easily distinguish the apparatus used in the experiment.

An important fact brought out by the above experiment is that an electrical stimulation strong enough to most violently stimulate the nervous system, as shown by the violent contractions of the muscular system, may still be too weak to produce phosphorescence. This fact gives a physiological confirmation of the morphological result stated above that no specific nerves are distributed to the phosphorescent organs.

I can explain the action of the electrical current in these experiments only on the supposition that it produces its effect by direct action on the gland.

The experiments just related were all tried on specimens of the fish taken from under the rocks where they were guarding the young brood. Two specimens, however, taken by hooks from the deeper water of Monterey bay, could not be made to show phosphorescence either by electrical stimulation or by treatment with ammonia. These specimens did not have the high development of the system of mucous cells of the skin exhibited by the nesting fish. My observations were, however, not numerous enough to more than suggest the possibility of a seasonal high development of the phosphorescent organs.

Two of the most important parts of the organ have to do with the physical manipulation of light — the reflector and the lens, respectively. The property of the reflector needs no discussion other than to call attention to its enormous development. The lens cells are composed of a highly refractive substance, and the part as a whole gives every evidence of light refraction and condensation. The form of the lens gives a theoretical condensation of light at a very short focus. That such is in reality the case, I have proved conclusively by examination of fresh material. If the fresh fish be exposed to direct sunlight, there is a reflected spot of intense light from each phosphorescent organ. This spot is constant in position with reference to the sun in whatever position the fish be turned and is lost if the lens be dissected away and only the reflector left. With needles and a simple microscope it is comparatively easy to free the lens from the surrounding tissue and to examine it directly. When thus freed and examined in normal saline, I have found by rough estimates that it condenses sunlight to a bright point a distance back of the lens of from one-fourth to one-half its diameter. I regret that I have been unable to make precise physical measurements.

The literature on the histological structure of known phosphorescent organs of fishes is rather meager and unsatisfactory. Von Lendenfeld describes twelve classes of phosphorescent organs from deep-sea fishes collected by the *Challenger* expedition. All of these, however, are greater or less modifications of one type. This type includes, according to von Lendenfeld's views, three essential parts, *i.e.*, a gland, phosphorescent cells, and a local ganglion. These parts may have added a reflector, a pigment layer, or both; and all these may be simple or compounded in various ways, giving rise to the twelve classes. Blood vessels and nerves are distributed to the glandular portion. Of the twelve classes direct ocular proof is given for one, *i.e.*, ocellar organs of Scopelus which were observed by Willemoes Suhm at night to shine "like a star in the net." Von Lendenfeld says that the gland produces a secretion, and he supposes the light or phosphorescence to be produced either by the "burning or consuming" of this secretion by the phosphorescent cells, or else by some substance produced by the phosphorescent cells. Furthermore, he says that the phosphorescent cells act at the "will of the fish" and are excited to action by the local ganglion.

Some of these statements and conclusions seem insufficiently grounded, as, for example, the supposed action of the phosphorescent cells, and especially the control of the ganglion over them. In the first place, the relation between the ganglion and the central nervous system in the forms described by von Lendenfeld is very obscure, and the structure described as a ganglion, to judge from the figures and the text descriptions, may be wrongly identified. At least it is scarcely safe to ascribe ganglionic function to a group of adult cells so poorly preserved that only nuclei are to be distinguished. In the second place, no structural character is shown to belong to the "phosphorescent cells" by which they may take part in the process ascribed to them.[1]

The action of the organs described by him may be explained on other grounds, and entirely independent of the so-called "ganglion cells" and of the "phosphorescent cells."

Phosphorescence as applied to the production of light by a living animal is, according to our present physiological-chemical notions, a chemical action, *an oxidation process*. The necessary conditions for producing it are two — an oxidizable substance that is luminous on oxidation, *i.e.*, a photogenic substance on the one hand, and the presence of free oxygen on the other. Every phosphorescent organ must have a mechanism for producing these two conditions; all other factors are only secondary and accessory. If the gland of a firefly can produce a substance that is oxidizable and luminous on oxidation, as shown as far back as 1828 by Faraday, and confirmed and extended recently by Watasé, it is conceivable, indeed probable, that phosphorescence in Scopelus and other deep-sea forms is produced in the same direct way, that is, by direct oxidation of the secretion of the gland found in each of at least ten of the twelve groups of organs described by von Lendenfeld. Free oxygen may be supplied directly from the blood in the capillaries distributed to the gland which he describes. The possibility of the regulation of the supply of blood carrying oxygen is analogous to what takes place in the firefly and is wholly adequate to account for any "flashes of light" "at the will of the fish."

In the phosphorescent organs of Porichthys, the only part the function of which cannot be explained on physical grounds is the group of cells called the gland. If the large granular cells of this portion of the structure (Pl. XXXVIII, Fig. 4, and Pl. XXXIX,[a] Figs. 5–7) produce a secretion, as seems probable from the character of the cells and their behavior toward reagents, and this substance be oxidizable and luminous in the presence of free oxygen, *i.e.*, photogenic, then we have the conditions necessary for a light-producing organ. The numerous capillaries distributed to the gland will supply free oxygen sufficient to meet the needs of the case. Light produced in the gland is ultimately all projected to the exterior, either directly from the luminous points in the gland or reflected outward by the reflector, the lens condensing all the rays into a definite pencil or slightly diverging cone. This explanation of the light-producing process rests on the assumption of a secretion product with certain specific characters. But comparing the organ with structures known to produce such a substance, *i.e.*, the glands of the firefly or the photospheres of Euphausia, it seems to me the assumption is not less certain than the assumption that twelve structures resembling each other in certain particulars have a common function to that proved for one only of the twelve.

---

[1] The cells which von Lendenfeld designates "phosphorescent cells" have as their peculiar characteristic a large, oval, highly refracting body imbedded in the protoplasm of the larger end of the clavate cells. These cells have nothing in common with the structure of the cells of the firefly known to be phosphorescent in nature. In fact, the true phosphorescent cells are more probably the "gland cells" found in ten of the twelve classes of organs which he describes.

I am inclined to the belief that whatever regulation of the action of the phosphorescent organ occurs is controlled by the regulation of the supply of free oxygen by the blood stream flowing through the organ; but, however this may be, the essential fact remains that the organs in Porichthys are true phosphorescent organs.

STANFORD UNIVERSITY, CAL.,
August 13, 1898.

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EXPLANATION OF PLATE XXXVIII.

FIGS. 1 and 2. Lateral and ventral view of the lines of phosphorescent organs and lateral-line organs in the adult of Porichthys notatus. The representation of organs is diagrammatic. Small circles show the location of phosphorescent organs, and the dots the lateral-line organs. I am indebted to my friend, Edward Hughes, for the outlines upon which these two figures are constructed.

a	anal.	*md*	mandibular.
br	branchiostegal.	*mx*	maxillary.
ca	caudal.	*oc*	occipital.
d	dorsal.	*op m*	operculo-mandibular.
d ac	dorsal accessory.	*pl*	pleural.
fr	frontal.	*sc*	scapular.
ga	gastric.	*sc ac*	scapular accessory.
ga gu	gastro-gular.	*sup o*	supraorbital.
gu	gular.	*t*	temporal.
la	lateral.	*u op*	upper opercular.
l op	lower opercular.	*v*	ventral.
ma	malar.		

FIG. 3. Lines and canals on the head. For explanation, see Figs. 1 and 2.

Figs. 4 to 24 are drawn with camera lucida. Figs. 4 to 8 represent the structure of adult phosphorescent organs, and Figs. 9 to 24 show the stages in the development of the phosphorescent organs of Porichthys notatus. The orientation of each organ with reference to the dorso-ventral plane of the fish is indicated by a short arrow pointing ventrally. Every section of epidermis shows numerous large mucous cells, many of which are empty.

FIG. 4. Cross-section of an adult organ in a new Porichthys from Panama. The gland shows several capillaries, all in cross-section but one. *l*, lens; *gl*, gland; *r*, reflector; *p*, pigment; *bl*, blood vessel.

EXPLANATION OF PLATE XXXIX.

FIG. 5. Cross-section of a ventral organ in Porichthys notatus Girard. *l*, lens; *gl*, gland; *r*, reflector; *bl*, blood vessels. In this section only a small amount of pigment shows to the left.

FIG. 6. Section of the deeper portion of a phosphorescent gland highly magnified to show the character of the cells. Flemming preparation.

FIG. 7. A somewhat oblique section of the deeper portion of a gland a little to one side of the center of an organ. Flemming preparation.

FIG. 8. The nerves distributed around the lens. Lens in outline. Golgi preparation.

FIGS. 9–11. Sections through a ventral, a pleural, and a lateral organ, respectively, of an embryo just before becoming free-swimming. The orientation of the organ with reference to the epidermis varies according to the position on the body. These three figures should follow in stage of development that shown in Fig. 24.

FIG. 12. Section of an embryonic organ just separating from the epidermis. This organ shows a differentiation even before it is cut off from the epidermis. Compare with Figs. 21 to 23.

EXPLANATION OF PLATE XL.^{a}

FIG. 13. Cross-section of a ventral organ at its first recognizable stage. Only a slight aggregation of cells in the basal layer of the ectoderm has appeared. This row is not associated with a lateral-line sense-organ Anlage. Embryo about 9 mm. long.

FIG. 14. Cross-section of gastric organ associated with sense-organ Anlage, *s an*. From the same embryo as Fig. 13.

FIG. 15. Cross-section of a pleural organ of an embryo 14 mm. long. The sensory Anlage shows to the left of organ.

FIG. 16. Section of a gular organ just external to the base of the ventral fin. Same embryo as Fig. 15.

FIG. 17. An organ from the same region as Fig. 16, but associated with a sense-organ.

FIG. 18. A pleural organ slightly older but from the same embryo as Fig. 15. *s an*, sensory Anlage.

FIG. 19. An inner anal organ beginning to separate from the epidermis. Same embryo as Fig. 15.

FIG. 20. Section through a pair of anal organs, showing a different degree of development. Same embryo as Fig. 15.

FIGS. 21 and 22. Organs in process of separation from the epidermis. Compare with Fig. 12.

FIGS. 23 and 24. Organs separated from the epidermis. The lens, *l*, and the gland, *gl*, are distinguishable, and the reflector, *r*, is forming from the connective tissue. Pigment cells, *p*, are arranged around the outside of the reflector.

CONTRIBUTIONS TO BIOLOGY
FROM
THE HOPKINS SEASIDE LABORATORY
OF THE
LELAND STANFORD JR. UNIVERSITY

XIX

NEW MALLOPHAGA, III.

Comprising

MALLOPHAGA FROM BIRDS OF PANAMA, BAJA CALIFORNIA AND ALASKA,

BY

VERNON L. KELLOGG,
Professor of Entomology, Leland Stanford Junior University.

MALLOPHAGA FROM BIRDS OF CALIFORNIA,

BY

VERNON L. KELLOGG AND BERTHA L. CHAPMAN.

THE ANATOMY OF THE MALLOPHAGA,

BY

ROBERT E. SNODGRASS,
Assistant in Entomology, Leland Stanford Junior University.

Reprinted from the
Occasional Papers of the California Academy of Sciences.—Vol. VI.

PALO ALTO, CALIFORNIA,
1899

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PALO ALTO, CALIFORNIA,
1899

PREFATORY NOTE.

This memoir is the nineteenth of a series designed to illustrate investigations and explorations connected with the Hopkins Seaside Laboratory, an adjunct of the biological laboratories of the Leland Stanford Junior University. These investigations have been carried on by means of the assistance given by Timothy Hopkins, Esq., of Menlo Park, California. This memoir appears in the publications of the California Academy of Sciences, the present edition being a reprint.

OLIVER P. JENKINS,
CHARLES H. GILBERT,
Directors Hopkins Laboratory.

Date of publication, February 28, 1899.

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AUTHOR'S PREFACE.

The papers presented herewith constitute the third contribution from the Entomological Laboratory of this University (Stanford) to the knowledge of the North American Mallophaga. The two previous papers are respectively, Kellogg, New Mallophaga, I, 1896[1] and Kellogg, New Mallophaga, II, 1896[1] and contain in addition to descriptions of species, an introduction to the study of the group, comprising keys to genera, terminology, bibliography, etc.

Mr. Snodgrass's paper presents the results of the first serious attempt to study comparatively the anatomy of these insects. There is yet needed to make the Mallophaga fairly known a study of their embryonic and post-embryonic life-history. It is hoped that this study can soon be undertaken.

Types of the new species described will be placed in the collections of this University, in the collections of the California Academy of Sciences, and in the collections of the University of Kansas. The authors have to express their obligations for services kindly rendered in connection with the preparation of this paper to Mr. Leverett M. Loomis, Curator of the Department of Ornithology, California Academy of Sciences, to Messrs. R. C. McGregor, J. F. Abbott, Cloudsley Rutter, A. W. Greeley, W. H. Osgood, J. C. Brown, R. C. McLain, R. W. Doane and E. M. Ehrhorn, to Prof. Walter E. Miller and to Miss Mary H. Wellman, artist.

V. L. K.

STANFORD UNIVERSITY,
April 15, 1897.

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[1] Proc. Cal. Acad. Sci., 2nd Ser., Vol. VI.

MALLOPHAGA FROM BIRDS OF PANAMA, BAJA CALIFORNIA, AND ALASKA.

(With Plates I-IV.)

BY VERNON L. KELLOGG.

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- Nirmus.
- Lipeurus.
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- Menopon.
- Physostomum.

List of Hosts, with Parasites.

INTRODUCTION.

The Mallophaga described and identified in this paper were collected by Mr. R. C. McGregor (from the Panama birds), by Mr. J. F. Abbott (from the Baja Californian birds) and by Messrs. Cloudsley Rutter and A. W. Greeley (from the Alaskan birds), all these collectors being students of Stanford University. The birds in each case were obtained personally by the collector, and the Mallophaga taken from the freshly killed specimens or newly made skins. The determinations of the Panama birds were made by Mr. Robert Ridgway, curator of birds, U. S. National Museum; the determinations of the Baja Californian birds by Mr. W. W. Price, student of Stanford University, and the determinations of the Alaskan birds by the collectors.

The sequence of genera in the following paper does not indicate the author's views with regard to the natural relationships of these genera, nor even with regard to the phyletic rank of the suborders. The Amblycerous genera, coming last in the present arrangement, are undoubtedly the more generalized of the two subordinal groups. The squence is that adopted in the European monographs and followed by me in my two previous papers (New Mallophaga, I, 1896, and New Mallophaga, II, 1896), and is retained for the sake of uniformity. The sequence of the species of each genus is determined by the host, the sequence of hosts being that adopted in the Check-List of North American Birds (2nd Edition, 1895), published by the American Ornithologists' Union. The names of the hosts are those used in the Check-List.

Wherever a species of Mallophaga is met, which has been previously identified by me on an American host, reference is made only to this previous identification, where the synonymy, European hosts, and figure and measurements of the species are given.

Docophorus.

Docophorous lari Denny. (See Kellogg, New Mallophaga, I, 1896, p. 98, pl. iv, fig. 4.)

Specimens from *Larus* sp. (Baja California) and from *Larus glaucescens* (North Pacific Ocean, off Alaska). Taken previously by me from several species of *Larus* (Bay of Monterey, California.)

Docophorus icterodes Nitzsch. (See Kellogg, New Mallophaga, I, 1896, p. 96, pl. iv, fig. 1).

Specimens from the Red-crested Merganser, *Merganser serrator* (Kodiak Island, Alaska). Previously taken by me from same host species and from seven other duck species (Kansas and California).

Docophorus cordiceps Giebel. (Plate I, fig. 2).

Insecta Epizoa, 1874, p. 103.

Docophorus glareolæ Giebel, Zeitschr. f. ges. Naturwiss., 1866, vol. xxviii, p. 312.

Docophorus nitzschia Giebel, Zeitschr. f. ges. Naturwiss., 1866, vol. xxviii, p. 312.

Docophorus mollis, Nitzsch (ed. Giebel), Zeitschr. f. ges. Naturwiss. 1861, vol. xviii, p. 312.

Docophorus frater Giebel, Insecta Epizoa, 1874, p. 103.

Docophorus cordiceps Giebel, Piaget, Les Pediculines, 1880, p. 80 and p. 664, pl. vi, fig. 2; Picaglia, Pediculini dell' istituto anat.-zool. d. R. Univ. d. Modena, 1885, reprint, p. 11.

A male, a female and a young specimen which may be referred to this species from *Tringa macularia* (Panama), and a male from *Tringa* sp. (Baja California). It is probable that Denny's *D. cephalus* (Monograph. Anoplur. Brit., p. 81, pl. ii, fig. 8; and Grube, Middendorff's Reise, 1851, p. 470) is this species.

The species may be recognized by its general dark coloration, broad head, short clypeus, and prominent and characteristic genitalia. I figure the male; Piaget has figured the female. The measurements of my specimens are as follows: male, body, length 1.6 mm., width .72 mm.; head, length .56 mm., width .62 mm.; female, body, length 1.65 mm., width .87 mm.; head, length .62 mm., width .75 mm.

Docophorus latifrons Nitzsch. (Plate I, figs. 5 and 8).

Germar's Mag. Entomol., 1818, vol. iii, p. 290.

Pediculus cuculi Fabricius, Syst. Ent., 1775, p. 807.

Pediculus fasciatus Scopoli, Entomol. Carniol, 1763, p. 383.
Docophorus latifrons N., Denny, Monograph. Anoplur. Brit., 1842, p. 97, pl. i, fig. 4; Giebel, Insecta Epizoa, 1874, p. 93; Piaget, Les Pediculines, 1880, p. 36, pl. ii, fig. 7.

Numerous specimens from a California Cuckoo, *Coccyzus americanus occidentalis* (Baja California), which are referable to this long-known *Docophorus* of the cuckoos, but on account of the markedly larger size, color differences, and other minor differences must be given a varietal name.

Var. *occidentalis* Kellogg. Male, body, length 2.06 mm., width .89 mm.; head, length .75 mm., width .75 mm. Female, body, length 2.5 mm., width 1.12 mm.; head, length .84 mm., width .85 mm. Piaget gives the following dimensions for *latifrons*: female, body, length 1.9 mm., width, .85 mm.; head, length .65 mm., width .6 mm. The male *latifrons* is 1.6 mm. long. My specimens have two long hairs on the temporal margins instead of one as described for *latifrons*, and have a distinct hair, not referred to in the descriptions of *latifrons*, in the posterior angles of the prothorax. The blotches on the ventral aspect of the abdomen of the males are with my specimens not oval, but transversely elongate, differing markedly from those of the female. The head and thorax of var. *occidentalis* are reddish brown, the ground color of the abdomen whitish, and the blotches blackish brown.

Docophorus californiensis Kellogg.

New Mallophaga, II, 1896, p. 483, pl. lxvi, fig. 6.

Eleven specimens from a Narrow-fronted Woodpecker, *Melanerpes formicivorous angustifrons* (Baja California). Type specimens taken from the Californian Woodpecker, *Melanerpes formicivorus bairdi* (Palo Alto, California).

Docophorus rufus n. sp. (Plate I, figs. 6 and 9).

A dozen specimens from the Ash-throated Flycatcher, *Myiarchus cinerascens nuttingi* (Baja California). A member, probably, of the group *femorati* of which *communis* is the chief representative. I have not found on my specimens the characteristic longish hair rising vertically from the dorsal surface of the anterior angles of the clypeus, but the broad clypeus, signature, genital blotches, and pustulated lateral abdominal blotches are of the *femorati* type. The species differs distinctly from *communis* in color, in the peculiar anterior convexity of the clypeus, in the extent of the transverse abdominal blotches, in the presence of transverse median blotches on the ventral aspect of the abdomen, and in the character of the genital blotches.

Description of the male. Body, length 1.56 mm., width .31 mm.; reddish brown, lighter on head and thorax, because the darker lateral abdominal blotches nearly cover the abdomen; broad headed; with ventral median transverse blotches on abdomen.

Head, length .5 mm., width .48 mm.; forehead broad, with expanded frontal uncolored part of clypeus flatly convex, with a shallow, median, curving emargination; no hairs on this frontal margin; sides of forehead with a pair of short hairs and a shorter single one in front of and near the trabeculæ; the trabeculæ very large, acute; antennæ when projected backward not quite reaching the occipital margin; the inconspicuous, slightly pendulous eyes with a hair, and two hairs on the flatly convex temporal margin; occipital margin nearly straight, bare; color, reddish brown; signature large, broad, anterior margin almost straight, the dark, sharp posterior point projecting beyond the mandibles;

antennal bands interrupted distinctly at the suture; occipital bands distinct, divergent, connected at base; ocular bands indistinct; trabeculæ weakly colored at base, uncolored distally; antennæ colored.

Prothorax quadrangular (as exposed), with a single hair in the posterior angles; posterior margin flatly convex; median part paler; lateral regions darker, and an indistinct posterior border. Metathorax rather short, posterior margin angulated, with a series of pustulated hairs; colored like the prothorax, paler in middle and with fairly distinct lateral borders. Legs concolorous with ground color of thorax, with small, darker, inconspicuous marginal markings. Sternal markings consisting of intercoxal lines and a very small median double blotch on prothorax. (Metathorax obscure).

Abdomen short, just as long as head and thorax; two to three long hairs in posterior angles of segments and numerous pustulated and other long hairs on dorsal surface; narrow, blackish, lateral bands; large dark brown lateral blotch, with clear stigmatal spots and about five pustulations along posterior margin, and leaving only a narrow median part of the abdomen uncovered; on segment 8 a complete transverse band; segment 9 rounded behind, with a narrow blackish posterior border, with a few longish hairs; genitalia showing through in segments 6–9; on ventral surface of segments 1-8 a large transverse median blotch reaching almost to the lateral margins.

Female. Body, length 1.94 mm., width .8 mm.; head, length .6 mm., width .56 mm.; the transverse blotches of abdomen but little smaller than those of male; segment 9 uncolored, with small brown lateral blotches, the posterior margin distinctly angularly emarginated;

ventral abdominal blotches smaller than those of male and not reaching so far laterally, those of posterior segments forming a genital blotch with broad, curving anterior part, narrower median part, and separate small lateral reniform parts.

Docophorus communis Nitzsch. (See Kellogg, New Mallophaga, II, 1896, p. 486, pl. lxvi, fig. 7).

Several specimens from the Saint Lucas Cardinal, *Cardinalis cardinalis igneus* (Baja California). Taken previously by me from 16 species of passerine birds (Kansas and California).

Docophorus panamensis n. sp. (Plate I, fig. 1).

From a tanagrine bird, *Phœnicothraupis fuscicauda* (Panama). A *Nirmus*-like form but with distinctly long trabeculæ. By shape of head and thorax allied to the *angustifrontes* group of the woodpeckers; resembling my *D. jungens* (New Mallophaga, II, 1896, p. 481, pl. lxvi, fig. 4) from *Colaptes auratus* (Kansas).

Description of female. Body, length 1.75 mm., width .61 mm.; narrow, Nirmoid, whitish with distinct brown lateral bands on thorax and abdomen, and quadrangular lateral transverse blotches.

Head, length .5 mm., width .5 mm.; triangular, with narrow front, slightly emarginated; three short hairs on each side of the anterior half of the forehead, and three longer hairs and a prickle in front of the trabeculæ; the trabeculæ prominent, extending beyond the tip of first segment of the antennæ; the antennæ rather thick, segment 2 longest, with a prominent short spiny hair; eyes rather large, with a prickle; temporal margin rounding, with one long hair and a few prickles; occipital margin slightly sinuous; forehead whitish with narrow brown antennal bands terminating at the suture; a palely colored broad suture with straight posterior margin and emarginated anterior border; whole hind head light brown with occipital margin very narrowly bordered with blackish brown.

Prothorax quadrangular, posterior angles rounded, with one hair, posterior margin flatly convex; whitish with dark brown lateral borders extending inward along the posterior margin. Metathorax angulated on abdomen, each latero-posterior side with nine long hairs (including the one in the lateral angle); lateral borders unevenly blackish brown; ground color of segment whitish tinged posteriorly with light brown, this posterior coloration interrupted by a median longitudinal whitish line. Legs very pale brown. Sternal markings consisting of distinct intercoxal lines, and faint traces of light brown median blotches.

Abdomen elongate-elliptical; a few longish hairs in posterior angles, and numerous weak long hairs on dorsal surface of segments in transverse series; ground color whitish with distinct, narrow lateral bands, darkest on anterior segments, and light brown, quadrangular, transverse lateral blotches on all segments, the two blotches of segment 8 meeting on the median line; segment 9 feebly emarginate, with no hairs on the posterior margin.

Docophorus domesticus Kellogg.

New Mallophaga, II, 1896, p. 475, pl. lxv, fig. 4.

A female and an immature specimen from the Black Martin, *Progne subis hesperus* (Baja California). Described from a Purple Martin, *Progne subis* (Lawrence, Kansas).

Docophorus laticeps Giebel. (Plate I, figs. 4 and 7).

Insecta Epizoa, 1874, p. 88.
Philopterus cincli Gervais, Hist. nat. d. Insectes aptères, 1847, p. 336.
Docophorus cincli Denny, Monograph. Anoplur. Brit., 1842, p. 85, pl. v, fig. 8.
Docophorus laticeps Giebel, Piaget, Les Pediculines, 1880, p. 65; Kœnig; Ein Beitrag zur Mallophagen-fauna, 1884, p. 3, pl. i, figs. 1-5; pl. ii, figs. 6, 7.

One adult female and two immature specimens from the American Dipper, *Cinclus mexicanus* (Kodiak Island, Alaska), which may be referred to this species, but which constitute a distinct variety characterized by the elongate, slender forehead with emarginated front. The species was found on *Cinclus aquaticus*, the European Dipper.

Var. *americanus* Kellogg. Female, body, length 2.06 mm., width .75 mm.; head, length .6 mm., width .5 mm.; thus being one-third longer than the species dimensions as given by Kœnig; head elongate, with narrow tapering forehead; front uncolored, with slight, narrowly rounded emargination; signature long, narrow, with posterior point reaching the mandibles; antennal bands distinct; trabeculæ long, slender; abdomen elongate-elliptical, with lateral triangular blotches with stigmatal spots and pustulations as in the species types; also, narrow blackish lateral bands; segment 8 wholly colored; ventral surface of abdomen with transverse median blotches; segment 7 with a narrower median blotch (touching blotch of segment 6) and two small lateral reniform blotches; segment 8 wholly colored or nearly so.

Docophorus rutteri n. sp. (Plate I, fig. 3).

A female and an immature specimen from an Oregon Chickadee, *Parus atri-capillus occidentalis* (Kodiak Island, Alaska). Denny has described two species of *Docophorus* from *Parus*, one, *pallescens* (Monograph. Anoplur. Brit., p. 82, pl. i, fig. 8) from *Parus palustris* and *P. major*, being based on immature specimens, and characterized by an emarginate clypeal front; the other, *pari* (ibid, p. 87, pl. vi, fig. 6) from *Parus caudatus*, *P. ater*, and *P. cœruleus*, being of chestnut ground color, without lateral abdominal blotches and with a subacuminate head, and without series of pustuled hairs along posterior margins of metathorax, in all of which diagnostic characters my specimen differs from *pari*. It agrees with it in hairy abdomen, acute trabeculæ, angulated metathorax, and general shape of abdomen.

Description of female. Body, length 2. mm., width .91 mm.; well marked with smoky brown blotches with large conspicuous pustulations, and many long hairs on dorsal aspect of abdomen.

Head, length .53 mm., width .6 mm.; a specially stiff, spiny short hair in each anterior angle of the flatly convex front, a hair before the suture and two before the trabeculæ; the trabeculæ long, slender, and weakly curving; antennæ when projecting backward barely reaching the occipital margin, with annulated segments; eye rather prominent, with a hair; a hair just behind the eye and three more on the rounded temporal angles; occipital margin weakly sinuous, the middle third slightly convex; signature large, distinct, with darker posterior acuminate point projecting beyond the mandibles, surrounded by a nearly uncolored region; antennal bands interrupted, widening at base; occipital bands distinct, blackish brown, diverging, and with anterior extremities reaching the blackish, distinct, curving, linear ocular blotches; region between the occipital bands pale; temples dark brown.

Prothorax small, short, margins rounding, with one long pustulated hair in posterior angle, another on posterior margin just a little inside of the angles, and four grouped together in the posterior median region of the segment; median region pale to uncolored, darkening laterally until the blackish lateral borders are reached. Metathorax roundly angulated on the abdomen; an unpustulated hair in the lateral angles and ten long hairs on each half of the posterior margin, rising from conspicuous pustulations; median region palest, lateral and posterior regions blackish brown, causing the clear pustulations to be very prominent. Legs smoky brown.

Abdomen oval; lateral angles projecting, with long hairs; dorsal surface of segments with single transverse series of long weak hairs; median region almost uncolored; prominent blackish brown, subtriangular, lateral, transverse blotches, with very conspicuous uncolored stigmatal spots and pustulations; segment 8 wholly colored, dark brown; segment 9 with small triangular lateral brown blotches; shallow, angular emargination behind.

Nirmus.

Nirmus punctatus Nitzsch. (See Kellogg, New Mallophaga, I, 1896, p. 109, pl. vi, figs. 1 and 2.)

Specimens from *Larus* sp. (Baja California). Taken previously by me from several species of *Larus* (Bay of Monterey, California).

Nirmus furvus Nitzsch. (Plate II, fig. 1).

Zeitschr. f. ges. Naturwiss. (ed. Giebel), 1866, vol. xxviii, p. 374.

Nirmus furvus N., Burmeister, Handb. d. Ent., 1832, vol. ii, p. 427; Giebel, Insecta Epizoa, 1874, p. 163, pl. v, figs. 2 and 3; Piaget, Les Pediculines, 1880, p. 169, pl. xiv, fig. 3; Supplement, 1885, p. 25; Osborn, Insects Affecting Domestic Animals, Bull. 5, N. S., Div. of Ent., U. S. Dept. Ag. 1896, p. 225.

A male and a female from the Spotted Sandpiper, *Actitis macularia* (Panama). My specimens do not possess the median longitudinal uncolored line across the first six or seven segments of the abdomen, as described for the types of the species, and besides, are very much darker, and are without distinct lateral transverse blotches on the abdominal segments. They are, too, a distinctly wider and less slender form, the head averaging nearly one-fifth wider in both sexes. However, in the present uncertain status of the species *furvus* (see Piaget, Les Pediculines, p. 170) I refer my specimens to the species, distinguishing them by a varietal name. Piaget's variety *alpha* (Supplement, p. 25) from *Vanellus cayensis* has, like my specimens, no uncolored median abdominal line, but no reference is made to any such characteristic dark chestnut to smoky general coloration of the body, as is shown by my specimens. Osborn's specimen is from *Phalaropus tricolor* (Museum Iowa Agricultural College).

Var. *ravus* Kellogg. Male, body, length 1.18 mm., width .34 mm.; head, length .37 mm., width .28 mm. Female, body, length 1.43 mm., width .37 mm.; head, length .40 mm., width .31 mm. Both sexes dark chestnut-brown to smoky, without median uncolored line on any abdominal segment, and without distinct abdominal blotches.

Nirmus fissus Nitzsch. (Plate II, fig. 2).

Germar's Mag. Entomol., 1818, vol. iii, p. 291.
Nirmus fissus N., Burmeister, Handb. d. Ent., 1835, vol. ii, p. 427; Denny, Monograph. Anoplur. Brit., 1842, p. 148, pl. x, fig. 6; Walckenær, Ins. Apt., 1844, vol. iii, p. 344.
Nirmus bicuspis N., Giebel, Insecta Epizoa, 1874, p. 155, pl. v, figs. 11 and 12; Piaget, Les Pediculines, 1880, p. 184, pl. xv, fig. 7.

Several specimens, including male, female and immature specimens, from *Tringa* sp. (Baja California). My specimens are larger than the types of *bicuspis* and offer distinct though minor differences. I have given them a varietal name.

Var. *major* Kellogg. Measurements. Male, body, length 1.61 mm., width .38 mm.; head, length .3 mm., width .31 mm. Female, body, length 1.87 mm., width .44 mm.; head, length .47 mm., width .33 mm. Differs from types of *fissus* (which were taken from "*Charadrius minor*") by having a hair in the eye, by having four pustulated hairs on each lateral half of the posterior margin of the metathorax instead of three, two being median and two being near the angle; by having the median longitudinal uncolored line of the abdomen limited to the first two segments, and by being markedly larger. Piaget's specimens of *fissus* are: length, male, 1.3 mm. to 1.4 mm.; female, 1.5 mm.

Nirmus fuscus Nitzsch. (See Kellogg, New Mallophaga, II, 1896, p. 499, pl. lxvii, fig. 7).

Many specimens from a Sparrow Hawk, *Falco sparverius* (Panama), a Lower Californian Sparrow Hawk, *Falco sparverius peninsularis*, a Duck Hawk, *Falco peregrinus anatum*, and a Saint Lucas Redtail, *Buteo borealis lucusanus* (Baja California). Taken previously by me from three species of hawks at Lawrence, Kansas. The size of these specimens from Panama and Baja Californian birds corresponds with that of the specimens previously taken by me from the Kansas birds, and is fully one-third greater than that recorded for the European specimens. The American specimens are at least varietally distinct from the typical Old World forms. There are variations manifest among the American specimens but I have not enough material yet to attempt to distinguish varieties.

Nirmus splendidus n. sp. (Plate II, figs. 3 and 6).

Males, females and young from a Caracara, *Polyborus cheriway* (Baja California). Species of *Docophorus*, *Lipeurus*, *Menopon*, and *Colpocephalum* have been taken from *Polyborus* by the European authors, but heretofore no *Nirmus*. The new species is unlike any of the *Nirmi* yet described from raptorial birds. It is large and strikingly marked.

Description of the male. Body, length 2.19 mm., width .84 mm.; large, broad-bodied, whitish with prominent lateral transverse brown abdominal blotches; head and thorax almost entirely colored.

Head, length .62 mm., width .6 mm.; forehead broad between trabeculæ and narrowly parabolic in front; forehead with four short separated hairs on each side; trabeculæ rather large for *Nirmus*, antennæ short; eye large, prominent, with a long hair, and with a fine prickle just behind it; temporal margins flatly convex, with two very long hairs; occipital margin straight; whole head strongly colored with exception of a pale, broad, clypeal, sutural line, and a short median longitudinal line leading from it backwards to the mandibles; the antennal bands narrow, and a little darker than general color of head, running entirely around frontal margin of head, although paler and nearly "interrupted" at the clypeal suture; trabeculæ nearly uncolored.

Prothorax short, oblong, with one hair in posterior angles; segment almost wholly colored. Metathorax short, the whole thorax being little more than one-half the length of the head; obtusely angulated on abdomen; posterior margin with a series of long hairs; segment mostly colored, darkest in median region; a broad white posterior border. Sternal markings consisting of inconspicuous intercoxal lines, and a small, indistinct median blotch on metathorax. Legs pale, though tinged with brown, with distinct, dark brown marginal markings.

Abdomen ovate; posterior angles of segments 1 and 2 without hairs, of segment 3 with a single hair, and of succeeding segments with two hairs; dorsal surface with numerous longish hairs; whitish with distinct lateral transverse blotches, each, with a clear stigmatal spot and some pustulations on segments 1–7; segment 8 with a curving, continuous brown transverse blotch; segment 9 rounded behind, with numerous longish hairs; uncolored except where the chitinized genitalia show through. Ventral surface all whitish except for a well defined and characteristic brown genital blotch on segments 7–9 (see fig. 6, pl. ii).

Female. Body, length 2.37 mm., width .97 mm.; head, length .62 mm., width .62 mm.; the increased size of the female is due to the larger abdomen, the head and thorax being of about the same size in both sexes; lateral abdominal blotches are not so long as in the male; segment 9 is shorter, bears two small blotches, and is slightly emarginated behind.

Nirmus atopus n. sp. (Plate II, fig. 4).

From a bird of the cuckoo family (Cuculidæ), *Piaya cayana thermophila* (Panama). This new form is one of the circumfasciate *Nirmi* of the general character of Rudow's *alchatæ* (Piaget, Les Pediculines, p. 165, pl. xiii, fig. 12) and allied forms. The few described members of this group have been found on columbine and gallinaceous birds.

Description of female. Body, length 1.84 mm., width .63 mm.; abdomen expanding posteriorly to segment 6; pale brownish white with brown lateral abdominal and thoracic bands and circumfasciate head.

Head, length .59 mm., width .53 mm.; forehead broad, rounded in front, with very few very fine hairs on the margin; trabeculæ small but distinct, acute; antennæ slender, with segment 5 longer than segments 3 or 4; temples rounded, with two long hairs and two or three very fine prickles on margins; eye without a hair, not especially prominent; occipital margin straight, bare; ground color of head whitish with small, inconspicous brown ocular blotches, temples very narrowly margined with brown, and rather broad chitin band, subtranslucent brownish along the entire front and lateral margins of forehead, and ending posteriorly in small elliptical expansions directed diagonally inwards.

Prothorax very short, quadrangular; lateral margins straight; posterior angles rounded, with one long hair; posterior margin straight; lateral borders brownish, the coloring extending along the posterior margin of the segment. Metathorax pentagonal, lateral margins bare, posterior margin obtusely angled on abdomen, with one hair in latero-posterior angle and four pustulated hairs in two pairs, one pair almost in the latero-posterior angle on each lateral half of the margin; lateral borders blackish brown, the color extending inward, but paling, in latero-posterior angles. Legs of pale ground color of the body, with narrow dark marginal markings. Sternal markings consisting of intercoxal lines, a small triangular blotch on mesothorax which fits like an apex to a larger pentagonal blotch on the metathorax.

Abdomen widening posteriorly to segment 6, then tapering bluntly; posterior segments with weak longish hairs in posterior angles; numerous weak, longish hairs on dorsal aspect in the broad median uncolored longitudinal line; lateral bands brown, distinct, extending posteriorly only through segment 7; pale brown, quadrangular, lateral, transverse blotches; last segment convex behind, with a very slight median emargination.

Nirmus virgatus n. sp. (Plate II. fig. 5).

Males and females from an icterine bird, *Amblycercus holosericeus* (Panama). Much like *N. illustris* Kellogg (New Mallophaga, II, p. 494, pl. lxvii, fig. 4), from the Red-winged Blackbird, *Agelaius phœniceus* (Lawrence, Kansas), and like *ornatissimus* Giebel (Insecta Epizoa, p. 144). The new form has a narrower front with the anterior angles not rounded, and does not possess the distinct bands internal to the antennal bands of the head of *illustris*. The lateral bands of the abdomen are wider, and the lateral transverse abdominal blotches are much more clearly indicated.

Description of male. Body, length 1.28 mm., width .47 mm.; whitish with striking broad black lateral borders of thorax and abdomen, black antennal and ocular bands, chestnut-brown outlines of transverse, lateral abdominal blotches on dorsal aspect, and chestnut-brown transverse median blotches on ventral aspect of abdomen.

Head, length .37 mm., width .37 mm.; front truncate or with a very shallow concavity; a few small hairs on sides of forehead; trabeculæ long; antennæ slender, segment 5 distinctly longer than either segments 3 or 4; eye distinct, slightly pendulous; temples not much expanded, margins flatly rounded, with one long hair and a few prickles; occipital margin straight; ground color whitish to uncolored; broad black antennal bands running to anterior angles of head and bending in angularly at base of trabeculæ; rest of forehead and trabeculæ uncolored; no colored clypeal signature; antennæ with segment 1 uncolored, other segments entirely blackish brown; ocular bands narrow, blackish; anterior part of temporal margins narrowly blackish; a brown, shield-shaped occipital signature showing through; mandibles and œsophageal sclerite showing through, brown.

Prothorax quadrangular, with rounded posterior angles with one hair in angle; segment whitish with broad lateral blackish brown borders. Metathorax angulated on abdomen; lateral angles obtuse; five long hairs on each latero-posterior margin; segment whitish, with uneven broad blackish lateral borders. Legs whitish with blackish brown blotches and semiannulations. Sternal markings consisting of distinct, chestnut-brown intercoxal lines, with expanded inner ends touching a small median blotch.

Abdomen elongate-ovate, with not very long hairs in posterior angles, and two hairs on the posterior margin of the dorsal aspect of each segment; ground color clear to whitish; broad lateral bands, from which project inwards the outlines of lateral transverse blotches which are oblong on segments 2–6, and tapering on segments 7–8; on the ventral aspect each segment has a chestnut-brown median blotch which shows through above; segments 8 and 9 are narrow; segment 9 projects narrowly backward, is narrowly but flatly rounded behind, and is mostly colored.

Female. Body, length 1.5 mm., width .53 mm.; head, length .41 mm., width .43 mm.; the head is a little wider in proportion to its length than in the male; last segment with distinct triangular lateral blotches and angularly emarginated behind.

Nirmus peninsularis n. sp. (Plate II, fig. 9).

Numerous specimens from a Phainopepla, *Phainopepla nitens* (Baja California). A member of the difficult group *interrupto-fasciati*, to which belongs my species *vulgatus* (New Mallophaga, II, p. 496, pl. lxvii, fig. 5), from seven passerine species, *simplex* (l.c., p. 492, pl. lxvii, fig. 2) from the Robin, *Merula migratoria*, and the strongly marked species *eustigmus* (l.c., p. 493, pl. lxvii, fig. 3) from Anna's Humming-bird, *Trochilus annæ*. The species from *Phainopepla* resembles most closely *brachythorax* Giebel (Insecta Epizoa, p. 134) from *Ampelis cedrorum*.

Description of female. Body, length 1.86 mm., width .41 mm.; long, slender, pale, with narrow marginal markings on head and intercoxal lines showing through on thorax.

Head, length .37 mm., width .31 mm.; elongate-triangular, with bluntly rounded apex; marginal hairs of forehead inconspicuous; trabeculæ small, uncolored but distinct; antennæ when projected backward reaching the occipital margin of head; eye not prominent, with a prickle; temples straight, with a single long hair in obtuse angle between temporal and occipital margin; occipital margin very flatly convex, ground color whitish; a blackish brown narrow lateral border on temples and forehead, this border turning in angularly at antennal fossa; front of clypeus uncolored and an indistinct, uncolored elongate-oval fossa widening posteriorly; mandibles and œsophageal sclerite showing through pale brown; no occipital border.

Prothorax quadrangular, with slightly convex, lateral and posterior margins; posterior angles with one small hair; ground color whitish, a blackish brown blotch in anterior angles, and posterior margin weakly bordered by the intercoxal lines of ventral surface showing through. Metathorax in outline a semicircle with anterior curving part slightly flattened and posterior margin slightly convex; posterior angles with three long pustulated hairs and three shorter, weaker, non-pustulated ones; one of the long hairs is in the apex of the angle, the other hairs are ranged along the posterior margin near the angle; segment whitish with darker anterior marginal markings. Sternal markings consisting of distinct intercoxal lines. Legs concolorous with thorax, with dark brown dorsal marginal markings.

Abdomen elongate, subparallel sided; segments 1 and 2 without hairs in posterior angles, segments 3–6 with one to two short, weak hairs in angles; segment 7 with three hairs in angles, and segments 8 and 9 with a few weak, curving hairs; segment 9 very short, with slight emargination; segments 5 and 6 with a hair on dorsal surface on each side rising from the posterior margin of segment just inward from the lateral band; dorsal surface otherwise naked; color of abdomen whitish, with narrow translucent lateral bands, each segmental portion passing the suture anteriorly.

Male. Body, length 1.34 mm., width .37 mm.; head, length .33 mm., width .26 mm.; being thus markedly shorter than the female; abdomen widening distinctly posteriorly, so that segment 5, which is widest, is more than one and one-half times as wide as segment 1; segment 8 short and much contracted within segment 7; segment 9 truncate behind; the genitalia showing indistinctly through segments 7–9; an indistinct, median pale brownish coloring on all segments.

Nirmus interpositus n. sp. (Plate II, fig. 7).

Three females from Vieillot's Warbler, *Dendroica bryanti* (Panama). A member of the group *interrupto-fasciati*, intermediate in markings between *N. vulgatus* Kellogg (New Mallophaga, II, p. 496, pl. lxvii, fig. 5), from several passerine birds from California and Kansas, and *eustigmus* Kellogg (l.c., p. 493, pl. lxvii, fig. 3), from *Trochilus annæ*, California. In size the new species is shorter than *vulgatus* but of the same width, and is both shorter and narrower than *eustigmus*. In general outline of body it resembles *eustigmus* more than *vulgatus*, but differs from *eustigmus* in having the sixth abdominal segment widest instead of the fourth.

Description of the female. Body, length 1.41 mm., width .41 mm.; whitish with distinct, broad, black, lateral abdominal bands and thoracic borders; head nearly equilaterally triangular.

Head, length .31 mm., width .34 mm.; outline of head nearly that of an equilateral triangle; the lateral margins of the head are weakly convex outward and the apex is parabolically curved; there are five or six short, inconspicuous hairs on each lateral margin of the forehead; the trabeculæ extend to the end of the first antennal segment and are uncolored; eye with a prickle; temporal margins with one long hair in the apex of the rounded, nearly right angle; occipital margin bare, very flatly convex; ground color whitish with a faint golden brown tinge; forehead and temporal margins narrowly bordered with blackish brown; front of clypeus uncolored; antennæ uncolored; occipital margin not bordered or only very narrowly and indistinctly so, an indistinct, pale brown, shield-shaped occipital signature showing through.

Prothorax very short, widely rectangular; a single longish hair in posterior angles; color whitish, with the intercoxal lines of under side showing through, and distinct blackish brown lateral borders. Metathorax short, lateral margins bare, sinuous; posterior margin flatly convex, with six or seven longish hairs on each half beginning in the posterior angle; whitish, with an uneven, blackish brown lateral border, and the strongly colored intercoxal lines of underside showing through. Legs whitish with blackish brown dorsal marginal markings. Sternal markings consisting of distinct intercoxal lines and indistinct pale median blotches.

Abdomen narrowest anteriorly, widening posteriorly to segment 4; segments 4–6 about same width, segment 7 slightly narrower, segments 8 and 9 short; short, weak single hairs in posterior angles of segments 3–7, with one or two shorter, weaker hairs in segments 5–7; dorsal surface with no or very inconspicuous hairs; whitish with distinct, rather broad, blackish brown lateral bands on segments 1–7, the segmental parts of the bands passing the suture and separated by nearly uncolored narrow spaces; covering the middle region of segments 6–7 a large, pale brown, shield-shaped blotch; segment

8 with a transvervse blotch, pale brown, darker outwardly, and behind not reaching the lateral margins; segment 9 with two very small pale brown linear lateral blotches, and feebly emarginated behind.

Nirmus audax n. sp. (Plate II, fig. 8).

From the yellow-headed Tit, *Auriparus flaviceps* (Baja California). A member of the group *interrupto-fasciati*, of darker ground color and with much more pronounced abdominal blotches than is usual in this group (see *vulgatus* Kellogg, New Mallophaga, II, 1896, p. 496, pl. lxvii, fig. 5).

Description of female. Body, length 1.6 mm., width .58 mm.; rather short and broad for *Nirmus*, especially of the *interrupto—fasciati* type; brownish ground with dark lateral blotches on thorax and abdomen, and blackish lateral bands and marginal markings.

Head, length .38 mm., width .41 mm.; the outline being nearly that of an equilateral triangle with blunted and curving apex and slightly convex legs; the marginal hairs of the forehead are few and very small; trabeculæ distinct, uncolored; temporal margins with a long hair in the rounded angle and several prickles; occipital margin weakly concave laterally and weakly convex in the middle; anterior part of forehead with nearly uncolored ground, with two brownish linear blotches bounding the oval fossa laterally; rest of head brownish with darker lateral borders and suggestions of occipital and ocular bands; antennæ colored.

Prothorax short, rectangular, with a single hair in posterior angles; color pale brownish in the middle, with the lateral regions dark brown, darkest on lateral margins. Metathorax angulated behind, with several strong hairs along each latero-posterior margin; latero-anterior margins bare, convex. Color brownish, paler in middle, stronger laterally and posteriorly, with uneven, blackish latero-anterior borders, and latero-posterior borders nearly uncolored. Legs brown with paler regions at extremities of segments and blackish dorsal margins, sternal markings consisting of distinct intercoxal lines, those between pro- and mesocoxæ with angulated spurs nearly touching; between the metacoxal lines a median blotch.

Abdomen short and broad, in shape an ellipse, segment 4 being the widest; ground color very pale brownish; segments 1–7 with narrow black lateral bands, the segmental parts distinct and passing the suture; quadrangular brown lateral blotches darkest internally on segments 1–7; segment 8 wholly colored; segment 9 uncolored and weakly emarginate behind; ventral surface of segments with a brown median blotch, the blotches of segments 6–7 fusing.

Lipeurus.

Lipeurus confidens n. sp. (Plate III, fig. 1).

Four females from a Black-footed Albatross, *Diomedea nigripes* (North Pacific Ocean). A species which in outline of body, color and markings is very like Piaget's species *tricolor* (Les Pediculines, p. 363, pl. xxx, fig. 4) from *Diomedea fuliginosa* (collection in the Museum of Leyden), but which is one and one-third times as large, without circumfasciate antennal bands, without occipital bands, with metathorax not without hairs as described for *tricolor* but with longish hairs in the posterior angles, without median abdominal blotches, and with last segment of female not acutely but bluntly two-pointed.

Description of female. Body, length 4.13 mm., width 1.03 mm.; large, whitish with sharply defined, black marginal markings, the lateral abdominal bands consisting of segmental pairs of contiguous subtriangular blotches.

Head, length .81 mm., width .7 mm.; subtriangular, widest just behind the eyes; front parabolic, with uncolored margin without hairs; a longish hair at the suture, with three in front of it (the foremost the longest) and two behind it on each side of the forehead; antennæ rather elongate, slender, segment 1 large and as long as segment 2; anterior angles of antennary fossæ acute but projecting little; the fossæ shallow; eyes prominent; temporal margins most convex just behind the eyes, obtusely angulated behind, and bearing a single weak hair and a few short spines; occipital margin nearly straight, bare; ground color whitish; strong, blackish brown antennal bands interrupted at the suture, widening posteriorly and extending back as far as the eye; two triangular blotches on occipital margins appearing as pointed continuations of the lateral bands of prothorax; antennæ uncolored.

Prothorax, as exposed, short, quadrangular, with flatly convex posterior margin and a longish spine in each posterior angle; color whitish, with even, strong, blackish lateral borders, turning in for a little distance at posterior angles. Metathorax with lateral concavities and five hairs in posterior angles, four of these hairs being long, strong, colored, and set closely together in a small uncolored space; posterior margin straight or even slightly concave; segment whitish with uneven, broad lateral borders, widest in middle and not reaching the posterior angles. Legs uncolored except for the chestnut-brown tarsi. No sternal markings.

Abdomen, fourth segment widest; segments of about equal length; posterior angles with few weak, not long, hairs; color whitish, with very narrow, clear lateral margin which sends expanded processes inward, three in each segment; the foremost of the three is the smallest and is contiguous to the suture; the hinder two are covered by two triangular blackish blotches which on some segments are contiguous, on others distinctly separate; segments 8 and 9 narrow, colored laterally; posterior margin of segment 9 truncate, with a very small angular emargination; two short hairs on each of the blunt points.

Lipeurus densus Kellogg. (Plate III, fig. 2).

New Mallophaga, I, 1896, p. 114, pl. vii, figs. 1 and 2.

A single male from a Black-footed Albatross, *Diomedea nigripes* (North Pacific Ocean, off Alaska). This specimen is a full millimeter longer and is much more completely blotched with dark brown than the original type specimen, a female; but I think they are of the same species. The female described is undoubtedly not fully grown and colored. While the antennæ vary in the sexes, that of the male bears no projection: it is simply heavier and larger, with its first segment largest; in the female, segment 3 is the longest. It is a male of this species, probably, which Taschenberg (Die Mallophagen, 1882, p. 145, pl. v, fig. 1*a*) describes and figures as the female of *ferox*.

Description of male. Body, length 5.8 mm., width 1.25 mm.; ground color very pale brown, but body mostly covered by large, dark brown blotches, head and thorax slightly longer than abdomen.

Head, length 1.3 mm., width 1.06 mm.; front parabolic, with a group of three distinct hairs at each side and two or three shorter ones along margin in front of antennary fossæ; antennæ large, long, (almost 1 mm.), without projection on any segment; segment 1 largest and other segments successively decreasing in width and length, uncolored except for an indefinite brownish annulation on segment 2; eyes projecting, conspicuous; temporal margins slightly expanded, rounded behind, with one short, weak hair and a few prickles; ground color brownish white; even, blackish brown antennal bands running around in front, the small portion of clypeus lying in front of the band being dark subtranslucent brown; temporal regions bounded within by diverging occipital bands, all blackish brown, these blotches acutely pointed in front and almost reaching to, but distinctly separate from, the bases of the antennal bands; on the forehead a dark brown lateral blotch on each side and in front of the mandibles.

Prothorax short and quadrangular as exposed; two short, weak hairs in posterior angles, one lying in on posterior margin; narrow median region of segment whitish, widest behind; lateral portions of segment blackish brown, paling inwardly. Metathorax large, long, with lateral margins concave, posterior margin weakly and flatly concave; a single short, weak hair in the apex of the posterior angles, and five longer, stronger, light brown hairs in a very small elongate-elliptical, uncolored space near the apex of the angles; segments all blackish brown, except a whitish, bluntly pointed, arrow-head-shaped, median region; projecting laterally from the posterior tip of this whitish space is on each side a small, linear, whitish space. Legs long, strong, coxæ nearly uncolored; femora dark brown, with uncolored extremities and tibiæ mostly colored. Sternal markings, prosternum with narrow, pericoxal lines; mesosternum with a rather large, brownish, median blotch; metasternum with weak indications of a median blotch.

Abdomen short, nowhere broader than thorax, with subparallel sides until segment 7 is reached, when the posterior tapering is begun; segments 1–6 of about equal size; segment 7 longer than others; segments 8–10 successively narrower and shorter; an uncolored median longitudinal line extending whole length of abdomen, rest of surface colored blackish brown by large quadrangular lateral blotches, which have clear stigmatal spots and are palest along inner margin; last segment angularly emarginated, with three short hairs on each point; segments 1–4 with a single very short hair in each posterior angle, segments 5–9 with longer hairs.

Lipeurus forficulatus Nitzsch. (See Kellogg, New Mallophaga, I, 1896, pl. ix, figs. 3, 4, 5 and 6).

Many specimens from a Californian Brown Pelican, *Pelecanus californicus* (Baja California). Taken previously by me from same host species (Bay of Monterey, California).

Lipeurus gracilicornis Piaget. (Plate III, fig. 3).

Les Pediculines, 1880, p. 309, pl. xxv, fig. 6.

Many specimens including males, females, and young from a Man o'War Bird, *Fregata aquila* (Panama). My specimens, to which I give a varietal name, differ from Piaget's types (taken from *Fregata minor*), as described, in three important particulars, viz., character of antennæ, metathoracic hairs, and size. In other particulars the specimens from the two bird species agree well.

Var. *major* Kellogg. Measurements (Piaget's measurements of the type specimens are in parentheses), male, body, length 3.12 mm. (2.5 mm.), width .37 mm. (.29 mm.); head, length .66 mm. (.58 mm.), width .39 mm. (.29 mm.) Female, body, length 3.10 mm. (2.4 mm.), width .69 mm. (.53 mm.); head, length .69 mm. (.63 mm.), width .50 mm. (.41 mm.) Distinctly larger than the types of the species; third segment of antenna of male with an appendage; metathorax with six long hairs, five together and one alone. I figure the female as Piaget has figured the male of the species type.

Lipeurus protervus n. sp. (Plate III, fig. 4).

Many specimens from a Willow Ptarmigan, *Lagopus lagopus* (Kodiak Island, North Pacific Ocean). On this Ptarmigan were some specimens of *Goniodes mammillatus* Rudow, found by me on the California Partridge, *Callipepla californica* (New Mallophaga, II, 1896, p. 509, pl. lxix fig. 2), but this *Lipeurus*, while of similar general character to *Lipeurus docophoroides* Piaget taken by me from *Callipepla californica* (New Mallophaga, II, 1896, p. 508, pl. lxviii, fig. 8), is distinctly of another species. The most readily noticeable difference is in the character of the lateral abdominal blotches, those of *docophoroides* leaving a comparatively wide, unblotched median region, while those of the new species leave but a narrow, median, unblotched line. The blotches of the first segment meet in the new species; they do not, even nearly, in *docophoroides*.

Description of female. Body, length 2 mm., width .72 mm.; short and broad, and sub-Docophoroid in form; whitish ground color with nearly completely colored head and thorax, and abdomen with large, lateral, quadrangular blotches.

Head, length .5 mm., width .5 mm.; front rounded, with four very small, inconspicuous hairs on each side; trabeculæ small, distinct, acute, uncolored; antennæ rather short, segment 2 longest, segment 5 longer than 3 or 4, segments 4 and 5 colored, others uncolored or very weakly colored; eye large, with a hair; temples widest just behind the eyes; temporal margins converging posteriorly, nearly straight, with two long hairs and prickles; occipital margin concave; head pale brown in median region, temples, occipital border, and antennal bands with rim around the front, dark brown; a pale, almost uncolored transversal linear space in front of the mouth, and a similarly pale U-shaped space bounding the median region of the hind-head.

Prothorax small, short, quadrangular as exposed, with a single long hair in each rounded posterior angle; segment wholly brown except an uncolored posterior border. Metathorax small, not as long as broad, posterior margin obtusely angled on abdomen; two long pustulated hairs in a clear space on posterior margin near the lateral angles and two long pustulated hairs in a clear space on posterior margin midway between lateral angles and posterior angles; whole segment brown except a small, angular, median, whitish or uncolored space on anterior margin. Legs pale brown with narrow dark brown marginal markings. Sternal markings consisting of intercoxal lines and a shield-shaped median blotch on metasternum.

Abdomen elliptical, posterior angles of segments projecting slightly and with one to two longish weak hairs; ground color whitish with large quadrangular lateral brown blotches on segments 1–7, these blotches nearly meeting inwardly and separated intersegmentally by a whitish space about one-half as large as a blotch; the outer margins of the blotches are blackish, forming narrow lateral bands; each blotch with a stigmatal spot, and a few (three or four) pustulations at inner end, in which are seated longish hairs; a long hair arises from a demi-pustulation on the posterior margin of each blotch just behind the stigmatal spot; segment 8 wholly colored and segment 9 nearly so; posterior margin of last segment minutely emarginated.

Lipeurus macgregori n. sp. (Plate III, figs. 5 and 6.)

Numerous specimens from three individuals of the Ani, *Crotophaga sulcirostris* (Panama). This striking *Lipeurus* with its small Nirmoid body, and, except for the antennæ, Docophoroid head, shows no near resemblance to any other *Lipeurus* so far described.

Description of the male. Body, length 1.81 mm., width .56 mm.; short and broad for *Lipeurus*, Nirmoid in shape, head with slightly expanded anterior border of clypeus uncolored, and slightly emarginated as with many *Docophori*; ground color of body whitish with strong, dark brown, lateral borders of head, and lateral, transverse blotches of thorax and abdomen.

Head, length .53 mm., width .47 mm.; thus nearly as broad as long, triangular, with sinuate sides and truncated apex; anterior border of clypeus slightly expanded, uncolored, feebly emarginate; seven or eight distinct, rather long hairs on lateral margin; an angular concavity on lateral margin midway between trabecula and anterior angle; trabeculæ prominent; antennary fossæ deep; eye prominent, almost pendulous, with a hair in it and a prickle just behind it; temporal margins convex, with three long hairs, a fourth one on occipital margin of temple; occipital margin sinuous, bare; antennæ long and large, segment 1 heavy, nearly as long as the rest of the segments together; segment

2 next largest and longest, segment 3 with simple appendage at distal extremity, segments 4 and 5 short, subequal; color whitish, with strongly colored, dark brown temples, angulated antennal bands, and lighter brown, distinct signature, pointed behind, straight in front; mandibles and œsophageal sclerite showing through dark brown; trabeculæ and antennæ paler smoky brown.

Prothorax short, quadrangular, wider than long, with one pustulated hair in posterior angle; a large, nearly square, dark brown, lateral transverse blotch nearly covering each lateral half of the segment, the broad, median line between them whitish. Metathorax short, but little longer than prothorax; posterior margin nearly straight, with five long pustulated hairs ranged along each lateral fourth, the inner two of the hairs may have only demi-pustulations. Sternal markings consisting of distinct, blackish brown intercoxal lines, and a pale brown, indistinct median blotch on metathorax. Legs pale smoky brown with darker margins and semiannulations.

Abdomen elongate-ovate; segment 1 conspicuously narrower than metathorax; one or two short hairs in posterior angles of anterior segments, two or three long hairs in angles of segments 5–9; ground color whitish with broad, dark brown, lateral, transverse blotches on segments 1–7, these blotches subquadrangular, but narrower inwards, and leaving only a broad, median, whitish, longitudinal line on middle of abdomen; in this whitish space a few longish hairs on each segment; rather large, uncolored, stigmatal spots in the transverse blotches of segments 2–7; the transverse blotch on segment 8 continuous across the segment and curving; segment 9 with two backward-projecting, short, horn-like processes, dark brown, and a narrowly rounded, uncolored posterior border; genitalia extending through segments 6–9 and strongly chitinized.

Female. Body, length 2.41 mm., width .78 mm.; head, length .6 mm., width .53 mm.; considerably larger; abdomen more elongate; antennæ rather long, slender, segment 2 longest; lateral, transverse blotches of abdomen less tapering inwards; blotches of segment 8 distinct; segment conspicuously emarginate behind.

Goniodes.

Goniodes mammillatus Rudow. (See Kellogg, New Mallophaga, II, 1896, p. 509, pl. lxix, fig. 2).

Specimens from the Ptarmigan, *Lagopus lagopus* (Kodiak Island, off Alaska). Previously taken by me from a Californian Partridge, *Callipepla californica* (Mountain View, California).

Eurymetopus.

Eurymetopus taurus Nitzsch. (See Kellogg, New Mallophaga I, 1896, p. 135, pl. xi, figs. 3, 4, 5 and 6).

Specimens from the Black-footed Albatross, *Diomedea nigripes* (North Pacific Ocean, off Alaska). Previously taken by me from *Diomedea albatrus* (Bay of Monterey, California).

Trinoton.

Trinoton luridum Nitzsch. (See Kellogg, New Mallophaga I, 1896, p. 152, pl. xiii, fig. 4).

Specimens from a Green-winged Teal, *Anas carolinensis* (Kodiak Island, off Alaska). Previously taken by me from same host species and six other duck species (Kansas and California).

Colpocephalum.

Colpocephalum abbotti n. sp. (Plate IV, fig. 9).

Taken from a gull, *Larus* sp. (Baja California). This new form is of the general type of *fuscipes* Piaget (Les Pediculines, p. 567, pl. xlvii, fig. 7) from *Larus dominicanus*, and of *funebre* Kellogg (New Mallophaga, I, p. 147, pl. xii, fig. 7) from *Larus glaucescens* (Bay of Monterey). It most nearly in general aspect, and especially in the branching, uncolored median line of abdomen, thorax, and head, resembles *sulcatum* Piaget (Les Pediculines, p. 565, pl. xlvii, fig. 5) from *Sterna nigra*, but is one-half larger, and has transverse series of hairs on the dorsal aspect of the abdomen, while *sulcatum* is here naked.

Description of female. Body, length 2.34 mm., width .88 mm.; rather large, long abdomen; abdomen sombre in color with narrow, black, lateral borders on hind head, thorax, and abdomen; a conspicuous, uncolored, median line on first five segments of abdomen, all of thorax, and hind head, the line dividing in the head and sending a branch to each lateral margin just in front of the ocular emargination.

Head, length .47 mm., width .7 mm.; front broad, very flatly convex, with numerous hairs of which four are longer than the others; on the lateral margins of the forehead in front of the ocular emargination a very long hair, with another shorter one close to it, and two in the angle; the palpi projecting beyond the lateral margins of the head; the ocular emargination deep, angular, with a prominent fringe and a longish hair rising just inward of the double eye; temples rather narrow, projecting, with four long hairs on the margin and one rising at some distance inward from the occipital margin; six uncolored spots on the forehead, from two of which single long hairs arise and from the remaining four short hairs; occipital margin flatly concave, bare; head smoky brown with narrow black occipital border and curved ocular blotches; a broad, short-stemmed, uncolored Y, the prongs slightly angulated in the middle and terminating broadly in front of the eyes; the stem interrupts the black occipital border and is continuous with a median, uncolored, longitudinal line which traverses the thorax and the first few abdominal segments.

Prothorax broader than long, with obtuse lateral angles containing one longish hair and a spine in the apex of the angle, and a second longish hair arising from a little within and back of the apex; the latero-posterior margins bare, with a single longish hair in the slight angle which may be taken to separate the latero-posterior margin from the true posterior margin; two longish hairs on each half of the flatly convex posterior margin; color smoky brown with narrow black border on latero-posterior margins and on visible parts of latero-anterior margins; the small, slightly curving, longitudinal chitin bars at ends of the indistinct, usual transverse bar are black; the ground color of the segment is darker in posterior half, and the segment is bisected longitudinally by the median, uncolored line Metathorax with a fairly distinct suture setting off the mesothorax; lateral margins bare; posterior angles with a hair and spines; posterior margin straight, with four weak hairs not on the very margin; color smoky brown with narrow black lateral borders. Legs slightly lighter than segments, and with ill-defined, darker marginal markings. Sternal markings distinct, a median shield on prothorax; a small, elongate, rather cone-shaped median blotch on mesothorax, and a large, broadly diamond-shaped, median blotch on metathorax; intercoxal lines between pro- and mesothorax distinct.

Abdomen elongate-elliptical; segments with a single long weak hair and some short ones in posterior angles, and some short ones along lateral margins; a single transverse series of not very closely set weak hairs along posterior margin of each segment; general color light smoky brown with very narrow blackish lateral bands; last segment parabolic behind, with short hairs, and at each side a few longish hairs.

Colpocephalum spineum n. sp. (Plate IV, fig. 1).

A single male from a Man o'War Bird, *Fregata aquila* (Panama). Piaget has taken a small *Colpocephalum* from *Fregata minor* (*angulaticeps*, Les Pediculines, p. 569, pl. xlvii, fig. 8), to which this new form must show some resemblance in size and characteristic quadrangular shape of forehead; but the shape of the abdomen, not at all elliptical as described for *angulaticeps*, but elongate-oblong with nearly parallel sides, and the distinct and characteristic abdominal markings and lateral hairs of the prothorax, serve to make any reference of my specimen to *angulaticeps* impossible.

Description of male. Body, length 1.53 mm., width .44 mm.; elongate, narrow, with subparallel sides; pale golden brown with large dark brown head blotches and lateral brown blotches on abdomen.

Head, length .34 mm., width .47 mm.; forehead nearly quadrangular, with a few short hairs along the front and four short ones and two longish ones on sides; palpi and antennæ slightly projecting beyond the margin of the head; temples broad with flatly convex lateral margins bearing numerous hairs of various lengths, two at least being long; occipital margin broadly concave; pale golden brown with broad blackish brown occipital border, greatly expanded triangularly at bases of the occipatal bands; ocular blotches large, and a distinct blotch on each side of the front rami of the mandibles extending diagonally to the front margin.

Prothorax short, with a spine and longish hair in each lateral angle and four longish hairs and two spines along each lateral half of the posterior margin. Metathorax longer and wider than prothorax, almost as wide as abdomen; several spines in a double row along the lateral margins, some strong spines in the lateral angles, and a series of ten or twelve strong hairs along the nearly straight posterior margin, whole thorax of pale brown ground color of body. Legs concolorous with the thorax, with dark brown markings near distal extremity of femur and on tibiæ. No distinct sternal markings.

Abdomen slender, elongate, with nearly parallel sides, with one long hair in posterior angles of segments 3–8 and numerous short hairs along lateral margins; dorsal surface covered with short spiny hairs, a series along the posterior margin of each segment being composed of longer but still spine-like hairs; color pale golden brown, the sutures whitish, and distinct subelliptical dark brown lateral blotches on segments 3–8, giving the abdomen a strikingly marked character; segment 9 but little narrower than segment 8 and broadly truncate behind; posterior margin with several long hairs and more shorter ones; dorsal surface with a transverse series of longish hairs.

Colpocephalum maculatum Piaget. (Plate IV, fig. 2).

Les Pediculines, 1880, p. 516, pl. xliii, fig. 1.

A male and a female from a Caracara,' *Polyborus cheriway* (Baja California), which I refer with much doubt to this species of Piaget, taken from a *Polyborus brasiliensis* (Zool. Garden of Rotterdam). Piaget says that *maculatum* much resembles *C. flavescens*, the common *Colpocephalum* of raptorial birds (see Kellogg, New Mallophaga, II, 1896, p. 525 pl. lxxi, fig. 4). My specimens do not resemble *flavescens* at all closely, lacking the cross bands of the abdomen, being rather differently shaped, etc. But Piaget's description and figure of *maculatum* show it also to differ from *flavescens* in these and other particulars. My specimens measure: Male, body, length 1.62 mm., width .66 mm.; head, length .34 mm., width .53 mm. Female, body, length 2. mm., width .72 mm.; head, length .34 mm., width .53 mm.

Colpocephalum subæquale Nitzsch. (See Kellogg, New Mallophaga, II, 1896, p. 525, pl. lxxii, fig. 1).

Specimens from an American Raven, *Corvus corax sinuatus* (Baja California). Taken previously by me from *Corvus americanus* (Palo Alto, California).

Colpocephalum diffusum n. sp. (Plate IV, figs. 3 and 4).

A well marked species found upon a surprisingly large number of widely related bird species from Panama. Mr. McGregor brought specimens from the following birds: *Amblycercus holosericeus*, *Arremonops striaticeps*, *Saltator albicollis*, *Phœnicothrampis fuscicauda*, *Elainea subpagana*, *Dendroica bryanti*, *Piaya cayana thermophila* (2 specimens), *Chiroxiphia lanceolata*, and *Ardea virescens* ! From the condition of affairs I should suspect straggling, but Mr. McGregor informs me that the birds were shot and the parasites collected on different days. We seem to have here a condition similar to the condition shown by *Docophorus communis*. In the list of hosts of this *Colpocephalum*, however, there are bird species of several unrelated families such as the Fringillidæ, Cuculidæ, Ardeidæ.

The specimens of the parasite vary somewhat in strength of color and hence distinctness of bands and blotches. Some of the weaker colored specimens, however, are evidently pupæ or freshly moulted adults. I have described the markings as shown in some well colored specimens from *Amblycercus holosericeus*.

Description of the male. Body, length 1.28 mm., width .53 mm.; ground color very pale, with distinct, blackish brown markings on head, thorax, and abdomen; transverse bands of abdomen uneven in size, the first and last bands being much larger than the middle ones.

Head, length .34 mm., width .47 mm.; a few short hairs on frontal margins; palpi barely projecting; ocular fringe distinct; temples broad, with a few long hairs; color whitish with prominent blackish ocular blotches projecting forward and connecting by a weakly colored, uneven broad line with the small but distinct blackish clypeal blotches; temples clear without dark margin; occipital margin narrowly bordered with blackish in the median part.

Prothorax; the part of the prothorax not concealed by the head is almost of the shape of a semicircle, a little flattened at the pole; the lateral angles lie very close to the occipital margin of the head, are obtuse, and bear three spines; there are three longish hairs on each lateral half of the rounded posterior margin; the segment is almost whitish with indications of darker borders and indistinct lines caused by the sternal markings showing through. Metathorax pentagonal, posterior margin straight, with four longish hairs and a spine (between the first two) on each lateral half; the posterior angles with two spines; color whitish with dark brown anterior angles, and sternal markings indistinctly showing through. Legs concolorous with thorax, with brownish and blackish markings. Sternal markings distinct, blackish brown, consisting of a median wedge-shaped blotch on prosternum connected by lateral processes with the intercoxal lines; a peculiar four-appendaged blotch on mesosternum composed of median blotch and meso-peri-coxal lines; and a pale median metasternal blotch with darker intercoxal lines.

Abdomen short, broadly elliptical, not turbinated; two or three distinct spines in posterior angles of segments; longish hairs in the angles and on the dorsal surface; segment 1 large; segments 2 and 3 not so large but larger than segments 4–7; segment 8 larger than segment 2 or segment 3; broad blackish brown lateral bands with the sutures distinct; no transverse bands on dorsal surface, but those of ventral surface showing through; these transversal bands arranged as follows: a single broad band covering all of segment 1 and anterior half of segment 2, narrow bands on segments 3–7, and one continuous band or blotch covering all of segments 8 and 9; the genitalia strongly chitinized, conspicuous, and extending through segments 2–9; last segment rounded behind, with a few short hairs; on the ventral surface of segment 2, a group of four very strong, long spines near each posterior angle.

Female. Body, length 1.56 mm., width .66 mm.; head, length .34 mm.; width .5 mm.; abdomen more elongate and the segments differently shaped; segment

1 very long, with straight posterior margin; segment 2 a little shorter, with distinctly curving posterior margin; segment 3 still shorter, with curving margin; segments 4–7 very short; segment 8 longer; ventral bands about as in male, with the last great band or blotch reaching anteriorly, with convex anterior margin, into segment 5.

Menopon.

Menopon titan var. **linearis** Kellogg.

New Mallophaga, I, 1896, p. 163, pl. xv, fig. 2.

Many specimens from a Californian Brown Pelican, *Pelecanus californicus* (Baja California). Described from same host species from Bay of Monterey, California.

Menopon auri-fasciatum n. sp. (Plate IV, fig. 5).

From a Man o' War Bird, *Fregata aquila* (Panama). Not at all like *M. intermedium* Piaget (Les Pediculines, p. 497, pl. xl, fig. 4) from *Fregata minor*.

Description of female. Body, length 2.19 mm., width 1.03 mm.; whitish with golden yellow transverse abdominal bands; dorsal surface of abdomen with many strong hairs in transverse series.

Head, length .31 mm., width .7 mm.; half-moon shaped, with smooth, even convex border; two short hairs on the front on each side of the middle, and two longish hairs and three shorter ones on each side in front of the antennal cavity; four very long hairs and several short ones in each temple; occipital margin concave, with six rather long hairs; pale yellowish white with black ocular flecks and small brown blotches just inside of the antennary cavities.

Prothorax rather large, with three short spines and a long hair along the narrowly rounded margin of the lateral angles, and five long hairs on each lateral half of the flatly rounding posterior margin; the lateral margins narrowly darker than the rest of segment, which presents no blotches; the uncolored transverse chitin bar is distinct, and the curving longitudinal bars at its extremities are darker than general color of segment. Metathorax as short as or shorter than prothorax, with very slight lateral emargination; lateral posterior angle with several small spines, and posterior margin, which is flatly convex, bears, beginning in lateral angles, two long hairs, then a spine, then eight long hairs, on each lateral half; a narrow transverse pale brown blotch runs across the segment near the posterior margin and expands at its lateral extremities. Legs of pale ground color of thorax with narrow darker marginal markings.

Abdomen ovate, rather turbinate, with longish hairs in the posterior angles of the segments and a single series of strong hairs across the dorsal aspect of each segment, ranged along the posterior margin of a pale brown transverse band which extends entirely across each segment; this band covers only about one-half the dorsal aspect of each segment, the uncovered half being of the whitish ground color of the general body, ninth segment flatly convex behind, with fringe of uncolored fine hairs, and with a few long hairs at lateral rounded angles.

Menopon striatum n. sp. (Plate IV, fig. 6).

Six specimens from a Willow Ptarmigan, *Lagopus lagopus* (Kodiak Island, North Pacific Ocean). Nearly twice as large as Grube's *M. lagopi* from *Lagopus alpinus*, though in general appearance the species must be similar. Grube describes the temples of *lagopi* with but one long hair; *striatum* has four, and the prothorax of *lagopi* is figured by Grube as being extraordinarily long.

Description of female. Body, length 2.22 mm., width .91 mm.; well marked, with entire transversal abdominal bands, with wide, whitish intersegmental spaces, and distinct, blackish, narrow lateral bands.

Head, length .3 mm., width .66 mm.; broadly parabolic in front, with slight rectangular orbital emargination; half a dozen short hairs on each lateral margin of forehead and three long hairs in region just in front of orbital emargination; the palpi projecting, as also the antennæ; temples narrow, five longish hairs, two more rising from occipital margin of temporal region; occipital margin concave, straight in the middle; ground color light brown, palest in median region, with very narrow blackish occipital border, blackish curving ocular blotches, and transversal dark brown bar in mandibular region.

Prothorax rather large, long; lateral angles obtuse, with three spines; posterior margin, from angle to angle, making a flattened semicircle and bearing 14 long hairs; ground color pale smoky brown, regions of lateral angles distinctly darker, transverse chitin bar dark, narrow, with a spine rising from each extremity; curving chitin bars at extremities of the transverse bar distinct, narrow. Metathorax with a broad whitish sutural space separating the small colored mesothoracic region from metathorax; metathorax with nearly straight posterior margin, and a series of hairs along straight posterior margin of broad chestnut-brown; transverse bar with narrow blackish lateral borders. Legs pale to smoky brown, with narrow, blackish dorsal marginings and conspicuous spiny hairs. Sternal markings consisting of pale brown linear transversal blotch on prosternum, distinct, narrow blackish diagonal intercoxal lines between pro- and mesolegs, with pale brown median triangular blotch emarginated on anterior margin, very pale, indistinct intercoxal lines between meso- and metalegs, with a pale brown triangular median blotch between them, and another smaller pale brown median blotch apparently between the metacoxæ, really on first abdominal segment.

Abdomen elongate-elliptical; two to three or four longish hairs in lateral angles of segments; on segments 1–8 a regular series of alternating whitish (sutural) and chestnut-brown transversal (segmental) bands, each colored band bearing a single series of longish hairs on small pustules along its posterior margin; a longer hair on larger pustule at each end of each of these series; narrow, segmentally interrupted blackish lateral bands, separated from the brown transverse bands by a narrow whitish space; segment 9 wholly chestnut-brown except pale to uncolored posterior border; posterior margin with thick-set fringe of uncolored longer and shorter hairs. Ventral surface of abdomen of segments 2–8 with a median pale brown transversal band, bearing numerous fine hairs rising from small pustules; segment 9 mostly colored.

Menopon præcursor n. sp. (Plate IV, fig. 8).

Many specimens from a Gila Woodpecker, *Melanerpes uropygialis* (Baja California). Denny is the only author who has hitherto described a *Menopon* from the woodpeckers (*M. pici*, from *Picus viridis*, Monograph. Anoplur. Brit. p. 219, pl. xx, fig. 5). From his brief description and strange illustration I cannot determine whether my specimens resemble his or not.

Description of the female. Body, length 1.56 mm., width .75 mm.; golden brown, with chestnut-brown transverse abdominal bands.

Head, length .28 mm., width .58 mm.; being thus twice as wide as long; very few short hairs along front; from a partly clear spot on the dorsal surface on each side of the forehead three hairs arise of which one is very long; the palpi project by the length of the terminal segment; no distinct ocular fringe; the temples narrow and bearing three very long hairs and two or three shorter ones; occipital margin weakly concave, with six longish hairs, two being median; ground color of head pale subtranslucent brown, with nearly uncolored temples; black ocular flecks, irregular brownish ocular blotches, and a very narrow blackish occipital border. On the ventral surface are two backward-projecting, segmented, pointed, chitinous processes arising apparently at about the origin of the labial palpi.

Prothorax large, the obtuse lateral angles projecting even with the insertion of the last of the three long occipital hairs; the lateral margins and posterior margin (separated by a very obtuse but obvious angulation) with a few longish, slightly pustulated hairs (two on each lateral margin and six on the posterior margin); a spine in each lateral angle; the regions of the lateral angles smoky, with narrow blackish border on lateral margin; the straight, transverse chitin bar uncolored, the curving, longitudinal chitin bars blackish; middle region of segment concolorous with middle region of head. Metathorax short, but little wider than prothorax; posterior margin straight, with a series of longish hairs; region of posterior angles and an indistinct transverse blotch entirely across segment darker. Legs concolorous with the pale ground color of the body, with very narrow darker dorsal margining. Sternal markings consisting of a narrow transversal median blotch on prosternum, and intercoxal lines curving backward at inner ends on mesosternum.

Abdomen rather short and broad, ovate; posterior angles projecting but slightly and bearing two to three long hairs; on the lateral margins of each segment a spine; a transverse series of hairs across each segment near its posterior margin; ground color very pale yellowish brown, with a chestnut-brown transverse band entirely across each segment except the ninth; posterior margin of segment 9 flatly angulated and with a close fringe of hairs.

Male. Body, length 1.34 mm., width .6 mm.; head, length .25 mm., width .53 mm.; the few specimens of males in the lot taken from the single bird examined are paler in color than the females; the transverse band of the eighth abdominal segment is hardly noticeable; segment 9 flatly rounded behind, with a few prominent hairs.

Physostomum.

With regard to the characters used in distiguishing species in this genus I am in much doubt. I believe that the genus is not at all well undertsood and that the specific determinations including my own (see New Mallophaga II, 1896, p. 513, *et. seq.*) need a thorough revision. This revision cannot, however, be undertaken until much more material is in hand. I describe the two following species with this doubt in mind, simply giving here as best I can additonal data, for the reviser. In the case of the two species here described, the unrelated hosts accredited to each suggest that we have to do in this genus with a few species of wide range of host, or with many species of very similar appearance.

Physostomum pallens n. sp. (Plate IV, fig. 7).

Specimens from a Prothonotary Warbler, *Protonotaria citrea* and from a Flycatcher, *Elainea subpagana* (Panama).

Description of female. Body, length 3.6 mm., width .87 mm.; pale buffy brown, with blackish brown head markings and thoracic markings and lateral abdominal bands.

Head, length .67 mm., width .66 mm.; front slightly expanded, flatly rounded; with laterally projecting palettes; several short prickle-like hairs in the slight ocular emargination; temples projecting backward, acute, with three long hairs, one on margin just behind the eye, and two close together on dorsal surface near the margin farther back; color whitish to clear with usual brown longitudinally arranged lateral blotches.

Prothorax hexagonal, front and posterior margins concave; a long hair and two spines in each lateral angle, and a long hair and two or three spines on each lateral margin near the posterior angles; lateral margins unevenly bordered with blackish brown, interrupted by a nearly uncolored spot in each lateral angle. Metathorax longer than prothorax, with straight posterior margin, and a single hair and spine in each posterior angle; a slight, rounded swelling behind anterior angles bearing spines; blackish brown, narrow, even, submarginal, longitudinal bands. Legs uncolored.

Abdomen parallel-sided, with a single hair and spine or prickle in posterior angles of segments; whitish with distinct, even, blackish brown submarginal longitudinal bands; vulva flatly rounded, with fringe of fine hairs; posterior margin of last segment flatly rounded, with fine, uncolored hairs.

Physostomum invadens n. sp.

Specimens from a woodpecker, *Melanerpes wagleri* and from *Chiroxiphia lanceolata* (Panama). The finding of this species on *Melanerpes* is the first recorded occurrence of *Physostomum* on a non-passerine bird.

Description of female. Body, length 3 mm., width .81 mm; pale translucent brownish with dark brown to blackish head and thoracic markings and lateral abdominal bands; in outline and structural characters very like *pallens*.

Head, length .66 mm., width .6 mm.; almost identical with that of *pallens*; ground color browner; the hairs of ocular emargination rather longer and fewer. Prothorax with lateral angles hardly apparent, but marked by the presence of a long hair and spine. Legs with a little brownish coloring. Abdomen with longer hairs and more in posterior angles of segments, and with two hairs on posterior margin of each segment just a little distance inward from posterior angle. Lateral bands of abdomen rather broad and marginal; in each of these broad brown longitudinal bands the true lateral bands, chitinized, may be seen.

LIST OF HOSTS, WITH PARASITES.

- Larus glaucescens
    - Docophorus lari
- Larus sp.
    - Docophorus lari.
    - Nirmus punctatus.
    - Colpocephalum abbotti.
- Diomedea nigripes.
    - Lipeurus confidens.
        - densus.
    - Eurymetopus taurus.
- Pelecanus californicus.
    - Lipeurus forficulatus.
    - Menopon titan var. linearis.
- Fregata aquila.
    - Lipeurus gracilicornis, var. major.
    - Colpocephalum spineum.
    - Menopon auri-fasciatum.
- Merganser serrator.
    - Docophorus icterodes.
- Anas carolinensis.
    - Trinoton luridum.
- Ardea virescens.
    - Colpocephalum diffusum.
- Tringa macularia.
    - Docophorus cordiceps.
    - Nirmus furvus var. ravus.
- Tringa sp.
    - Nirmus fissus var. major.
- Lagopus lagopus.
    - Lipeurus protervus.
    - Goniodes mammillatus.
    - Menopon striatum.
- Polyborus cheriway.
    - Nirmus splendidus.
    - Colpocephalum maculatum.
- Falco sparverius peninsularis.
    - Nirmus fuscus.
- Crotophaga sulcirostris.
    - Lipeurus macgregori.
- Coccyzus americanus occidentalis.
    - Docophorus latifrons var. occidentalis.
- Piaya cayana thermophila.
    - Nirmus atopus.
    - Colpocephalum diffusum.
- Melanerpes wagleri.
    - Physostomum invadens.
- Melanerpes uropygialis.
    - Menopon præcursor.
- Melanerpes formicivorus angustifrons.
    - Docophorus californiensis.
- Myiarchus cinerascens nuttingi.
    - Docophorus rufus.
- Elainea subpagana.
    - Physostomum pallens.
    - Colpocephalum diffusum.
- Corvus corax sinuatus.
    - Colpocephalum subæquale.
- Amblycercus holosericeus.
    - Nirmus virgatus.
    - Colpocephalum diffusum.
- Arremonops striaticeps.
    - Colpocephalum diffusum.
- Saltator albicollis.
    - Colpocephalum diffusum.
- Chiroxiphia lanceolata.
    - Physostomum invadens.
    - Colpocephalum diffusum.
- Cardinalis cardinalis igneus.
    - Docophorus communis.
- Phœnicothraupis fuscicauda.
    - Docophorus panamensis.
    - Colpocephalum diffusum.
- Progne subis hesperus.
    - Docophorus domesticus.
- Phainopepla nitens.
    - Nirmus peninsularis.
- Protonotaria citrea.
    - Physostomum pallens.
- Dendroica bryanti.
    - Nirmus interpositus.
    - Colpocephalum diffusum.
- Cinclus mexicanus.
    - Docophorus laticeps var. americanus.
- Parus atri-capillus occidentalis.
    - Docophorus rutteri.
- Auriparus flaviceps.
    - Nirmus audax.

EXPLANATION OF PLATES.

PLATE I.—Fig. 1, *Docophorus panamensis* Kellogg, ♀. Fig. 2, *D. cordiceps* Giebel, ♂. Fig. 3, *D. rutteri* Kellogg, ♀. Fig. 4, *D. laticeps* G., var. *americanus* Kellogg, ♀. Fig. 5, *D. latifrons* N., var. *occidentalis* Kellogg, ♀. Fig. 6, *D. rufus* Kellogg, ♀. Fig. 7, *D. laticeps* G., outline of head. Fig. 8, *D. latifrons* N., var. *occidentalis* Kellogg, abdomen of ♂, ventral aspect. Fig. 9, *D. rufus* Kellogg, abdomen of ♀, ventral aspect.

PLATE II.—Fig. 1, *Nirmus furvus* N., var. *ravus* Kellogg, ♀. Fig. 2, *N. fissus* N., var. *major* Kellogg, ♀. Fig. 3, *N. splendidus* Kellogg, ♀. Fig. 4, *N. atopus* Kellogg, ♀. Fig. 5, *N. virgatus* Kellogg, ♀. Fig. 6, *N. splendidus* Kellogg, genital blotch of ♂. Fig. 7, *N. interpositus* Kellogg, ♀. Fig. 8, *N. audax* Kellogg, ♀. Fig. 9, *N. peninsularis* Kellogg, ♀.

PLATE III.—Fig. 1, *Lipeurus confidens* Kellogg, ♀. Fig. 2, *L. densus* Kellogg, head of ♂. Fig. 3, *L. gracilicornis* P., var. *major* Kellogg, ♂. Fig. 4, *L. protervus* Kellogg, ♀. Fig. 5, *L. macgregori* Kellogg, head of ♂. Fig. 6, *L. macgregori* Kellogg, ♀.

PLATE IV. Fig. 1, *Colpocephalum spineum* Kellogg, ♂. Fig. 2, *C. maculatum* P., ♂. Fig. 3, *C. diffusum* Kellogg, ♂. Fig. 4, *C. diffusum* Kellogg, ventral aspect of abdomen of ♀. Fig. 5, *Menopon auri-fasciatum* Kellogg, ♀. Fig. 6, *M. striatum* Kellogg, ♀. Fig. 7, *Physostomum pallens* Kellogg, ♀. Fig. 8, *Menopon præcursor* Kellogg, ♀. Fig. 9, *Colpocephalum abbotti* Kellogg, ♀.

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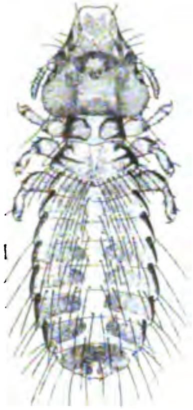

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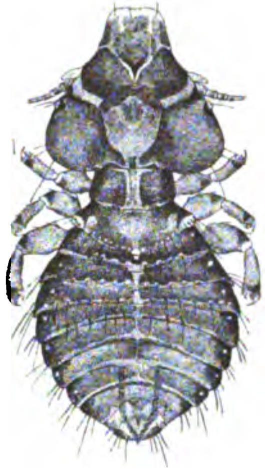

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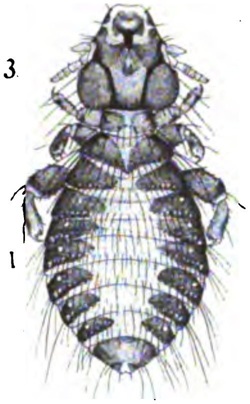

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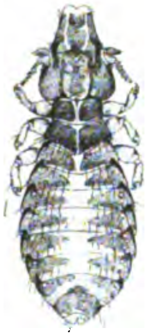

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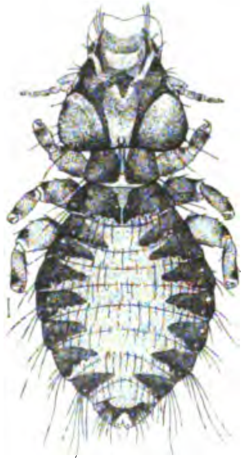

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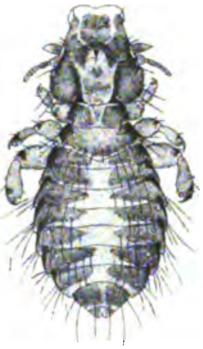

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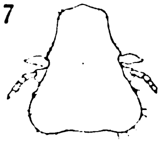

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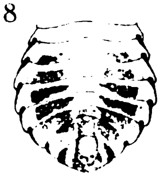

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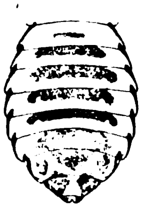

Mary Wellman del.

Lith Britton & Rey S.F.

Oc. Papers, Cal. Acad. Sci. Vol. VI. [Kellogg] Plate II.

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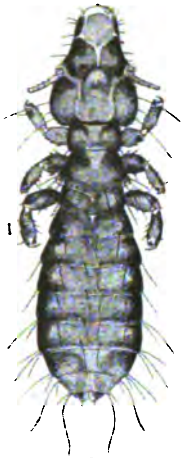

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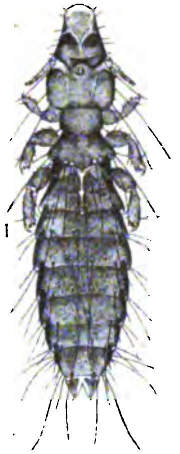

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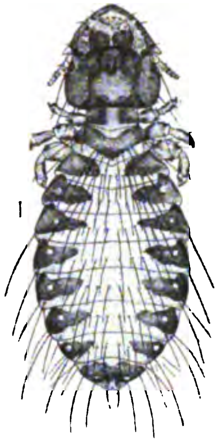

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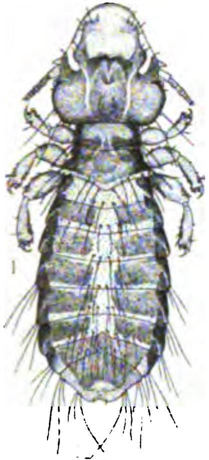

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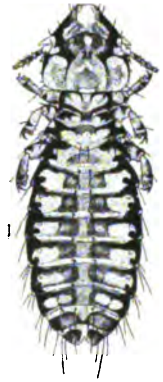

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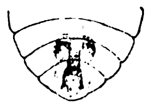

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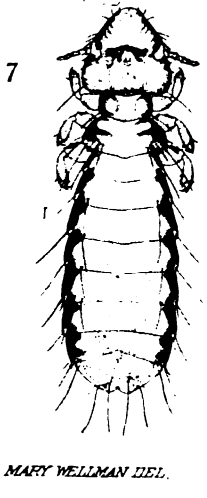

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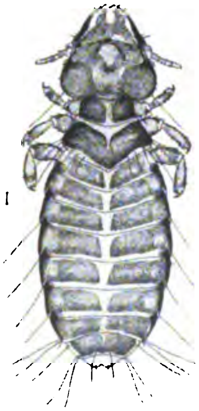

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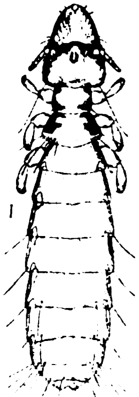

MARY WELLMAN DEL.

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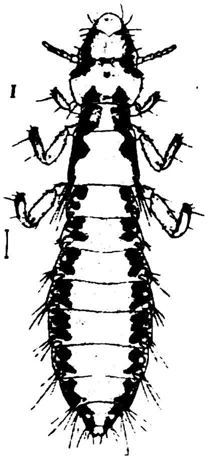

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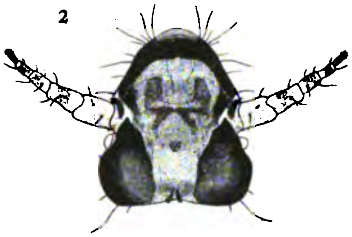

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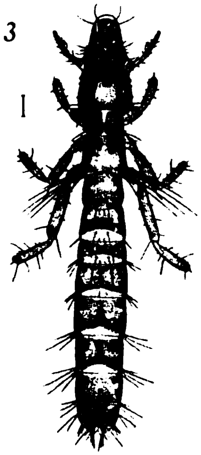

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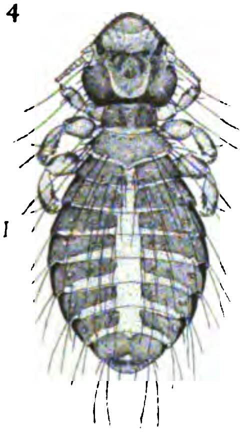

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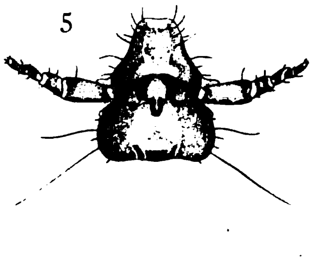

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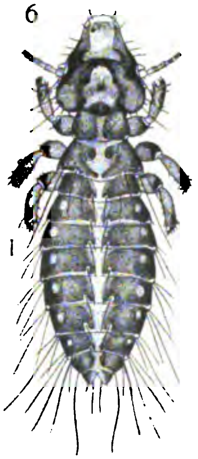

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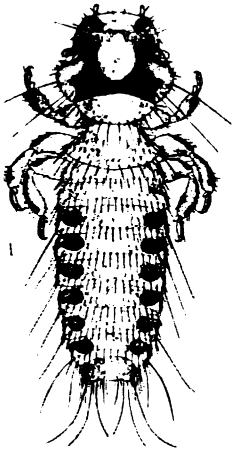

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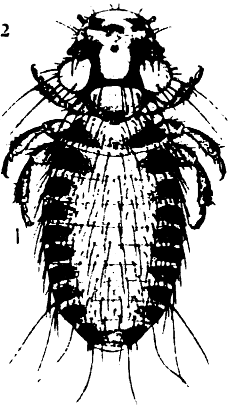

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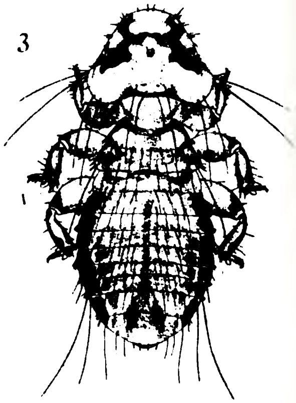

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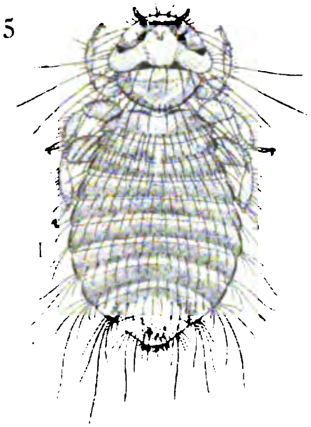

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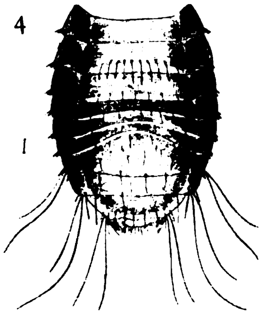

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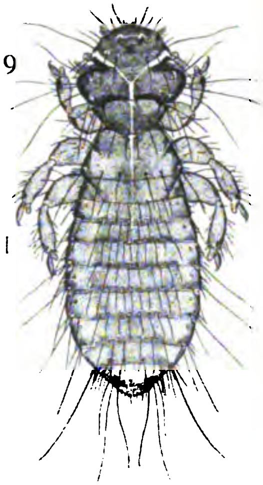

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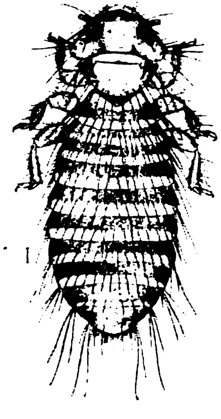

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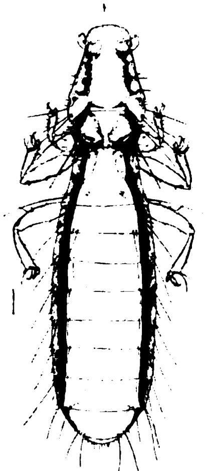

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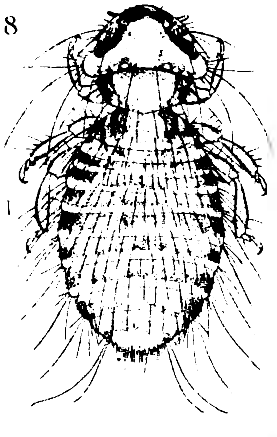

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LITH BRITTON & REY S.F

MALLOPHAGA FROM BIRDS OF CALIFORNIA.

(With Plates V to IX.)

BY VERNON L. KELLOGG AND BERTHA L. CHAPMAN.

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INTRODUCTION.

The Mallophaga described and referred to in this paper were collected by Messrs. Snodgrass, Osgood, Brown, and McLain, students of Stanford University, California, Mr. Ed. M. Ehrhorn, Horticultural Commissioner for Santa Clara County, California, and by the senior author, Mr. Kellogg. All of the specimens from birds of the Bay of Monterey, California, were taken by Mr. Kellogg from just-killed birds or freshly made skins collected by Mr. Leverett M. Loomis, Curator of the Department of Ornithology, California Academy of Sciences. The authors desire to acknowledge their obligations to these various collectors.

The sequence of genera in this paper is that adopted in the European monographs and in the papers of the senior author (Kellogg, New Mallophaga I, 1896;* New Mallophaga II, 1896;* Mallophaga from Birds of

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* Proc. Cal. Acad. Sci., 2d. Ser. Vol. VI.

Panama, Baja California, and Alaska, in New Mallophaga III, 1899). The sequence of species in each genus is determined by the hosts, the sequence of hosts being that of the A. O. U. Check-List of North American Birds, 2d. edition, 1895.

Docophorus.

Docophorus procax n. sp. (Plate V, fig. 1).

Many specimens from two Pigeon Guillemots, *Cepphus columba* (Bay of Monterey, California). A member of the group *trianguliferi* Piaget (Les Pediculines, p. 113), and most resembling *pilosus* Piaget (ibid, p. 116, pl. x, fig. 4) from a flamingo, *Phœnicopterus antiquorum*, but differing in the hairs of clypeus, of metathorax, shape of abdominal blotches, etc.

Description of the male. Body, length 1.45 mm., width .76 mm.; head comparatively large, with frontal part of clypeus uncolored and expanded; thorax and first segment of abdomen golden brown with darker markings; abdomen oval, pale, whitish medially, with dark brown transverse bands and blackish lateral bands.

Head, length .52 mm., width .54 mm.; conical, temples wide, sides rapidly approaching each other anteriorly; frontal uncolored clypeal space expanded; front straight or feebly concave; no hairs on the rounding uncolored clypeal region but one short marginal prickle at the point where the clypeus begins to swell beyond the sides of the head; a second short prickle before the suture; two dorsal hairs just before the clear uncolored clypeal region; two short prickles in front of the trabeculæ; trabeculæ large, reaching nearly to the end of the second segment of the antennæ, well colored with pale brown, a short prickle at the base; antennæ small, of the same golden brown as the head, with slightly darker markings; eye inconspicuous, with two short prickles and an ocular fleck; temples rounded, with two long hairs and several prickles; occipital margin straight; clypeal signature broadly shield-shaped, sides constricted anteriorly, with posterior angle reaching almost to the mandibles; the quadrangular space in the middle of the signature is slightly darker than the most anterior portion; antennal bands interrupted by the suture, the bands turning in at the suture, nearly meeting on the median line, the bands themselves becoming narrow and acuminate; the posterior ends of the antennal bands bend in and back till they meet the dark blotch caused by the mandibles showing through the head; ocular blotches distinct; temporal borders narrow, occipital bands distinct, slightly diverging anteriorly; occipital border not extending to the sides of the head.

Prothorax broad, with sides diverging; posterior angles rounding; lateral borders dark, extending in along the posterior margin. Metathorax pentagonal, sides strongly divergent, posterior margin angular, with slightly rounding tip on the abdomen; one short prickle and one long pustulated hair in the posterior angles, three pustulated hairs each side of the posterior marginal angle; segment pale in the middle, growing darker laterally and posteriorly. Legs of the same golden brown as the thorax, darker lateral borders and annulations, claws also dark. Sternal markings consist of dark brown intercoxal lines and a pale median metathoracic blotch.

Abdomen broadly ovate, turbinated; segments 2 to 7 with prominent posterior angles, each bearing from one to three long hairs; segment 1 wholly golden brown, the transverse blotches meeting near the posterior margin in an acute point; the transverse lateral blotches of segments 2 to 7 are separated by a transparent whitish median space; the lateral margins of the segments are dark brown to black; along the posterior margins of the transverse lateral bands are partially uncolored spots bearing long hairs; stigmatal spots distinct; segment 8 wholly pale brown, darker in the middle, owing to the dark genitalia showing through; segment 9 very small and uncolored; genitalia distinct, dark brown reaching as far forward as segment 6.

Female. Body, length 1.62 mm., width .78 mm.; head, length .56 mm., width .53 mm.; abdomen not so broad in comparison with the length as in the male, not turbinated, and the median whitish space larger.

Docophorus lari Denny. (See Kellogg, New Mallophaga, I, 1896, p. 98, pl. iv, fig. 4).

Specimens from *Larus delewarensis*, *L. occidentalis* (three birds), and *L. heermanni* (two birds) (Bay of Monterey, California). Previously taken by Kellogg from these and other species of *Larus*.

Docophorus melanocephalus Burmeister. (See Kellogg, New Mallophaga, I, 1896, p. 99, pl. iv, fig. 6).

Two specimens from the Royal Tern, *Sterna maxima* (Bay of Monterey, California), and two specimens from the Pomarine Jaeger, *Stercorarius pomarinus* (Bay of Monterey, California). Previously taken by Kellogg from *Sterna maxima* (same locality).

Docophorus validus n. sp. (Plate V, fig. 2).

A single female specimen of this striking *Docophorus* from a Black-vented Shearwater, *Puffinus opisthomelas*

(Bay of Monterey, California). In general shape and in certain special characters this new form somewhat resembles *D. brevi-antennatus* Piaget (Les Pediculines, p. 108, pl. ix, fig. 9) from *Sula australis* (Museum of Leyden); the differences, however, in shape of metathorax, abdominal blotches, etc., are marked.

Description of the female. Body, length 2.25 mm., width 1.18 mm.; large triangular head with narrow, emarginate front; abdomen nearly circular, with strongly marked, lateral, transverse blotches, mostly acute inwardly.

Head, length .72 mm., width .72 mm., front of the head before the trabeculæ elongate and markedly narrowing anteriorly; dark lateral margins extending slightly beyond the narrow, concave, uncolored clypeal region, terminating in a sharp, slightly incurving angle; a short prickle on the anterior margin of this projecting angle, a short hair on the lateral margin of the front, near the suture; two dorsal hairs extending beyond the lateral margin of the head; trabeculæ large, reaching to the end of the second segment of the antennæ; segment 1 of the antenna long, segment 5 but little longer than segments 3 or 4; eyes prominent, with a short spine and a hair; temples slightly protruding, parabolic, with two long hairs and three short spines; occipital margin slightly convex upon the prothorax; signature distinct, anteriorly concave; deeper chestnut-brown along the anterior margin than through the wide median portion, posteriorly narrowing into a dark, narrow, acuminate point reaching to the mandibles; the anterior portion of this posterior point is darker than the rest of the signature; antennal bands broad, even, of a dark, rich, golden brown, paling slightly in the anterior portion, beyond the suture; posterior extremities bending inwardly, separated by a pale median space between the occipital bands; occipital bands much paler than the temporal borders, indistinctly fading anteriorly into dark ocular blotches; temporal margins narrowly bordered with dark brown; occipital blotches distinct.

Prothorax small, oblong; angles rounding, with one long hair; lateral blotches distinct, separated by a pale median line, darker along the posterior margin near the angle, and fading gradually anteriorly. Metathorax only two-thirds as wide as the head, with strongly diverging sides, rounding, posterior angles; posterior margin broadly rounded upon the abdomen; one very short prickle and one long hair in a pale brown space on the posterior angle; six long pustulated hairs on the posterior margin; lateral markings little darker than the general dark brown of the metathorax.

Abdomen nearly circular; transverse, lateral blotches distinct, acute inwardly, and darkest at the inner ends; each bearing from one to four pustulated hairs; segment 8 entirely dark brown; segment 9 rounding, with a narrow, angular emargination; one fine hair each side of this emargination.

Docophorus icterodes Nitzsch. (See Kellogg, New Mallophaga, I, 1896, p. 96, pl. iv, fig. 1).

Specimens from a Lesser Scaup Duck, *Aythya affinis*, and from an American Scaup Duck, *Aythya marila nearctica* (Palo Alto, California). Previously taken by Kellogg from the first named host species, and from six other duck species.

Docophorus fusiformis Denny. (Plate V, fig. 3).

Monographia Anoplurorum Britanniæ, 1842, p. 84, pl. i, fig. 2.

Docophorus fusiformis D., Giebel, Insecta Epizoa, 1874, p. 104; Piaget, Les Pediculines, 1880, p. 86, pl. vi, fig. 7.

Docophorus fissiformis D., Osborn, Insects Affecting Domestic Animals, Bull. 5, N. S., Div. of Ent., U. S. Dept. Ag., 1896, p. 217.

One male from a Least Sandpiper, *Tringa minutilla* (Palo Alto, California). Denny's specimens were taken from the same host; Giebel's single specimen from the same host, and Piaget's from *Tringa subarquata*. Osborn's specimens are from the "black-billed sandpiper" (Burnett collection). Our specimen has no emargination of the clypeal front, a character especially noted by Denny and Piaget. But Giebel's specimen is like ours: "der Vorderrand ist nicht tief ausgeschnitten, sondern nur sanft concav." The species can be recognized by the large elongate head, the dark coloration, and narrow genitalia. Our specimen, figured, measures: body, length, 1.31 mm., width .5 mm.; head, length .5 mm., width .44 mm.

Docophorus fuliginosus Kellogg.

New Mallophaga, I, 1896, p. 80, pl. iii, fig. 2.

Specimens from the Black-bellied Plover, *Squatarola squatarola*, and from the Semipalmated Plover, *Ægialitis semipalmata* (Pacific Grove, California). Described from *Squatarola squatarola* (Kansas and California).

Docophorus pictus Giebel. (Plate V, fig. 4).

Insecta Epizoa, 1874, p. 74.

Docophorus pictus G., Piaget, Les Pediculines, 1880, p. 23.

Numerous specimens from a Golden Eagle, *Aquila chrysaëtos* (Palo Alto, California). The specimens are of the characteristic group infesting eagles, of which *platystomus* N. (Giebel, Insecta Epizoa, p. 69, pl. ix, fig. 1; Piaget, Les Pediculines, p. 17, pl. i, fig. 1) may be taken as type. So many species have been described in this group, on what seems to us slight differences, that one may well despair of making a satisfactory reference of his specimens to any one of the forms to the exclusion of all others. From this same host half a dozen species of *Docophorus* (all of the *platystomus* type) have been described.

The truncate, not emarginated, clypeal front, and the slight dilation of the uncolored part of the clypeus lead us to refer our specimens to a species proposed by Giebel for specimens collected from the same host as that of our specimens. Osborn (Insects Affecting Domestic Animals, 1896, p. 218,) describes a species *halieti* from the Bald Eagle, *Haliæetus leucocephalus* (Florida). This species has a marked lateral, anterior, clypeal dilation, and the front is emarginate.

The members of the group may be recognized by the uncolored front of the clypeus more or less dilated. We figure a female. Measurements: Male, body, length 2.22 mm., width 1.2 mm.; head, length .85 mm., width .91 mm. Female, body, length 2.81 mm., width 1.4 mm.; head, length .94 mm., width 1. mm.

Docophorus cursor Nitzsch. (See Kellogg, New Mallophaga, II, 1896, p. 484, pl. lxvi, fig. 1).

Specimens from two individuals of the American Long-eared Owl, *Asio wilsonianus*, (Ontario, California). Taken previously by Kellogg from *Bubo virginianus* (Lawrence, Kansas). Recorded by Osborn from *Asio wilsonianus* (Ames, Iowa, and Lincoln, Nebraska).

Docophorus speotyti Osborn.

Insects Affecting Domestic Animals, 1896, Bull. No. 5, Div. o Ent., U. S. Dept. Ag., p. 222, fig. 144.

Specimens from a Spotted Owl, *Syrnium nebulosum* (La Honda, California). Agrees well with Osborn's description (except that the abdomen is narrow, with subparallel sides in the *female*, while it is more elliptical, widest at segment 4, in the *male*, just the reverse of the condition according to Osborn).

Docophorus ceblebrachys Nitzsch. (See Kellogg, New Mallophaga, II, 1896, p. 485, pl. lxvi, fig 3).

Many specimens from a Snowy Owl, *Nyctea nyctea* (Pullman, Washington). Taken previously by Kellogg from same host (Kansas).

Docophorus singularis n. sp. (Plate V, fig. 5).

Specimens from a Nuttall's Woodpecker, *Dryobates nuttallii* (Ione, California). Not like any other woodpecker-infesting *Docophori*, but belongs rather to the group *femorati*.

Description of the female. Body, length 1.43 mm., width .71 mm.; dark chestnut-brown with distinct bands on the head and thorax, angular, lateral, transverse blotches on the abdomen; unique in the possession of bipartite trabeculæ.

Head, length .65 mm., width .53 mm.; large, broadly concave, uncolored clypeal region broad with straight to slightly concave front; one marginal hair in front of distinct suture, two dorsal hairs near the lateral margin, one rather short and stiff, extending forward beyond the clypeal margin, the second very long; two dorsal hairs in front of the trabeculæ; the trabeculæ divided, anterior part short and acutely angulated, extending around the base of the posterior portion of the trabeculæ on the ventral surface, the posterior portion of the trabeculæ nearly as long as the first two segments of the antennæ, about the same width throughout, a deep chestnut-brown at the base, with uncolored tip; antennæ with the first two joints long and about equal, pale golden brown, last three joints darker chestnut-brown, a few short spines on the joints, especially numerous and strong on the first two joints; eye with one long hair, and near the posterior margin a second long hair; temples rounding, with three long, pustulated, marginal hairs and one short prickle, occipital margin slightly convex; signature distinct, anterior margin concave, with a slight lateral constriction near the anterior angles, posterior angles extended backward, posterior margin extending in a long, acute angle beyond the mandibles; antennal bands distinctly interrupted at the suture, dark chestnut-brown, posterior extremities inward and back, meeting well defined, diverging occipital bands; temples dark chestnut-brown, with narrow blackish margins, interrupted by large pustulations.

Prothorax small, lateral margins strongly rounding; one long pustulated hair in the posterior angle; lateral blotches dark chestnut-brown, separated by a pale median line; blackish lateral borders. Metathorax with strongly divergent lateral margins nearly as wide as the head; a series of long pustulated hairs on the angulated posterior margin; lateral blotches dark, separated by a pale median line which widens distinctly near the middle; bands of blackish brown on the lateral and posterior margins. Sternal markings composed only of the distinct intercoxal lines between the pro- and mesothoracic legs. Legs pale brown with dark bands.

Abdomen broadly ovate, segments distinctly narrowing on the median line; one to three long hairs in the posterior angles; many long, pustulated, dorsal hairs in a transverse series on the posterior margin of each segment; lateral transverse triangular blotches dark chestnut-brown, slightly darker on the lateral margin; median portion of the abdomen uncolored; posterior margin of the transverse blotches interrupted by uncolored pustulations; segment 8 entirely dark brown;

segment 9 narrowly emarginate, rounding, with two short prickles on the posterior margin; two dark lateral blotches separated by a broad uncolored space; genital blotches distinctly dark brown, broadly rounding on segments 5 and 6, posterior margin rapidly tapering to segment 8.

Male same size as female; last segment broadly, flatly rounded, with several long hairs on each side of the bare median third of the posterior margin.

Docophorus californiensis Kellogg.

New Mallophaga, II, 1896, p. 483, pl. lxvi, fig. 6.

Specimens from Williamson's Woodpecker, *Sphyrapicus thyroideus* (El Dorado county, California), the White-headed Woodpecker, *Xenopicus albolarvatus* (El Dorado county, and Kings River Cañon, California), and the Californian Woodpecker, *Melanerpes formicivorus bairdi* (Palo Alto, California). Types collected by Kellogg from *Melanerpes formicivorus bairdi* (Palo Alto, California). The specimens from the El Dorado county birds show narrow heads and bodies, but this is probably due to shrinking in drying, as all the specimens of the small collections from this locality appear to have suffered in the same way.

Docophorus rufus Kellogg.

Mallophaga from Birds of Panama, Baja California and Alaska, in New Mallophaga, III, 1899, p. 7, pl. i, figs. 6 and 9.

Three specimens from an Ash-throated Flycatcher, *Myiarchus cinerascens* (Alameda county, California) and three specimens from another specimen of the same bird species from Ontario, California. Described by Kellogg from *Myiarchus cinerascens nuttingi* (Baja California).

Docophorus fusco-ventralis Osborn.

Insects Affecting Domestic Animals, 1896, Bull. 5, N. S., Div of Ent., U. S. Dept. of Ag., p. 221.

One specimen from an Ash-throated Flycatcher, *Myiarchus cinerascens* (Palo Alto, California). Osborn's specimens were from the Wood Pewee, *Contopus virens* (Cornell University Collection; Burnett Collection).

Agrees well with Osborn's description, except that the fuscous coloration of ventral aspect is in broad transverse bands separated by distinct, paler sutural bands, instead of being "beneath uniformly dark brown."

Docophorus communis. (See Kellogg, New Mallophaga, II, 1896, p. 486, pl. lxvi, fig. 7).

Under this name we group together a large number of very similar forms; or if dissimilar, forms connected by gradatory specimens. These forms are taken from passerine birds and belong to Piaget's group *femorati* (Les Pediculines, p. 53), characterized by the large truncate or feebly convex or weakly emarginated clypeus, with long hair in each anterior angle, by the especially large third pair of legs, and by the conspicuous pustulated hairs of the thorax and abdomen. The marked variation (notably in size of hindmost legs) among individuals from a single bird specimen (let alone bird species) and the series of gradatory forms connecting all the variations manifest in the group make it impossible for us to attempt to distinguish different species in this mass of material. Piaget has, indeed, attempted to define half a dozen varieties of *communis*, but in no very confident manner. The group *femorati* can furnish time-killing work for any student bold enough to undertake its discipline.

Docophori of this group, referable to the species *communis*, in its widest sense, have been determined by us from the following passerine hosts, all from California: Ash-throated Flycatcher, *Myiarchus cinerascens*; Western Flycatcher, *Empidonax difficilis*, two specimens; Mexican Horned Lark, *Otocoris alpestris chrysolœma*; Blue-fronted Jay, *Cyanocitta stelleri frontalis*, three specimens; California Jay, *Aphelocoma californica*; Western Meadow Lark, *Sturnella magna neglecta*; Brewer's Blackbird, *Scolecophagus cyanocephalus;* Pine Siskin, *Spinus pinus;* Western Lark Sparrow, *Chondestes grammacus strigatus*, two specimens; Intermediate Sparrow, *Zonotrichia leucophrys intermedia;* Gambel's Sparrow, *Zonotrichia leucophrys gambelii*, three specimens; Golden-crowned Sparrow, *Zonotrichia coronata*, two specimens; *Spizella* sp.; Western Chipping Sparrow, *Spizella socialis arizonæ;* Bell's Sparrow, *Amphispiza belli;* Samuel's Song Sparrow, *Melospiza fasciata samuelis*, two specimens; California Towhee, *Pipilo fuscus crissalis*, two specimens; Black-headed Grosbeak, *Zamelodia melanocephala;* Western Blue Grosbeak, *Guiraca cœrulea eurhyncha*, three specimens: Louisiana Tanager, *Piranga ludoviciana*, two specimens; Cedar Waxwing, *Ampelis cedrorum;* Northern Shrike, *Lanius borealis;* California Shrike, *Lanius ludovicianus gambeli*, two specimens; Cassin's Vireo, *Vireo solitarius cassinii;* Yellow Warbler, *Dendroica œstiva*; Vigor's Wren, *Thryothorus bewickii spilurus;* Plain Titmouse, *Parus inornatus*, three specimens; Audubon's Hermit Thrush, *Turdus aonalaschkœ auduboni;* Western Bluebird, *Sialia mexicana occidentalis.* Previously taken by Kellogg from sixteen species of passerine birds.

Docophorus mirinotatus n. sp. (Plate V, fig. 6).

A female and several immature specimens from a Thurber's Junco, *Junco hyemalis thurberi* (Goat Mt., alt. 11,500 ft., Kings River Cañon, California). This Nirmoid form does not much resemble any other *Docophorus* known to us. The strangely emarginated, transverse abdominal blotches are unique.

Description of the female. Body, length 1.65 mm., width .53 mm., slender, Nirmoid in form, with head wider than thorax and almost as wide as abdomen; abdomen yellowish white, with narrow blackish lateral bands, and transverse bands with their anterior margins widely and irregularly emarginated.

Head, length .46 mm., width .43 mm.; clypeus broad, with straight or very slightly concave front; one short hair in the lateral margin near the front, a second longer hair in front of the suture; eye with a long hair; temples flatly rounding, with two very long hairs and two or three prickles; markings indistinct; antennal bands interrupted at the suture; occipital bands widely separated posteriorly but converging rapidly anteriorly, forming a triangle with the mandibles at apex; trabeculæ slender, short.

Prothorax narrow, quadrangular, with a long hair in the posterior angle; pale medially, with distinct dark lateral bands. Metathorax with a series of long hairs along the posterior margin which is distinctly angulated on the abdomen; lateral, dark brown borders.

Abdomen slender, elongate-elliptical; from one to three long hairs in the posterior angles of the segments and a dorsal, transverse series of long pustulated hairs on each segment rising near the middle of the segments; segments with median blotches which are widely and irregularly emarginate anteriorly, the blotches also interrupted by the pustulations which fade into the medial emargination; the transverse blotches distinctly darker on the posterior margin just beneath the uncolored medial space and extending laterally not quite to the lateral bands; distinct narrow blackish bands on the lateral margins; last segment narrowly, angularly emarginate, with a short hair on the posterior margin each side of the emargination, and with pale brown transverse blotches, but no dark bands on lateral margins.

Docophorus mirus n. sp. (Plate V, fig. 7).

A few specimens from two Vigor's Wrens, *Thryothorus bewickii spilurus* (Palo Alto, California). Characterized by the very large head and small abdomen, the head being two-fifths as long as the whole body and almost, if not quite, as wide.

Description of the female. Body, length 1.5 mm., width .65 mm.; head very large in proportion to the body, five-sixths as wide as the abdomen and two-thirds as long.

Head, length .56 mm., width .53 mm., broadly conical; uncolored clypeal front slightly concave in the middle, a rather long stiff dorsal hair rising near the lateral margin and extending forward beyond the margin of the head, a short hair on the margin in front of a distinct suture, two rather long hairs before the trabeculæ which reach as far as the end of the second segment of the antennæ; segment 2 of the antennæ long, segment 5 longer than either segment 3 or 4; eye distinct, a long hair on the dorsal surface and a shorter hair arising near the posterior angle; three long hairs and a short prickle on the rounding angle of the temples; occipital margin slightly convex; signature distinct, pale fulvous, anterior margin slightly concave; lateral margins straight, though the dark, narrow lines of the inner bands make it appear that there is a strong constriction near the anterior margin; posterior angles rounding; posterior margin extending back beyond the mandibles in a dark, narrow point; antennal bands marginal, narrow, dark chestnut-brown, interrupted by the distinct suture, bending in to meet the anterior ends of the occipital bands in an indefinite, pale fulvous band; temples bordered anteriorly with a narrow border of dark chestnut; occipital bands narrow but distinct posteriorly, widely diverging and apparently connecting with the antennal bands.

Prothorax narrow, about half as wide as the head; lateral margin convex, one long pustulated hair in the posterior angles; a narrow lateral border of dark chestnut-brown. Metathorax with sides convex and strongly diverging; a series of long pustulated hairs on the posterior margin which is obtusely angled on the abdomen; lateral margin bordered with dark chestnut-brown. Legs fuscous, with dark fuscous borders and semiannulations; third pair of legs conspicuously large; a few scattered hairs and spines.

Abdomen broadly ovoid, short in comparison with the large head; first three segments longer than the others, their posterior margins more nearly straight; segments 4 to 8 narrowed, especially in the middle; last segment narrowly emarginate; many long pustulated hairs on the abdomen arranged in series on the posterior margin of each segment, especially thick along the middle; three or four short prickles on the lateral margin of the emargination of the last segment; first four segments dark chestnut-brown, segments 5 to 9 paler fuscous.

Male. Body, length 1.46 mm., width .53 mm.; head, length .53 mm., width .5 mm.; last abdominal segment rounded, with a fringe of about ten rather long weak hairs.

Nirmus.

Nirmus fusco-marginatus Denny. (Plate V, fig. 9).

Monograph. Anoplur. Brit., 1842, p. 136, pl. x, fig. 1.
Nirmus fusco-marginatus D., Giebel, Insecta Epizoa, 1874, p. 178; Piaget, Les Pediculines, 1880, p. 202, pl. xvi, fig. 6.

Many specimens of a *Nirmus* which may be referred to as a variety of this species of Denny, from an American Eared Grebe, *Colymbus nigricollis californicus;* also two specimens (rather smaller) from two Pigeon Guillemots, *Cepphus columba*, and a single specimen from the American Herring Gull, *Larus argentatus smithsonianus* (all the birds from the Bay of Monterey, California). Denny's types were taken from *Podiceps auritus* (Ireland), and Piaget's specimens from *Podiceps cristatus.* It seems to me that the *Nirmus podicipis* of Denny (Monograph. Anoplur. Brit. p. 142, pl. x, fig. 9) and the *Lipeurus runcinatus* Nitzsch (Giebel, Insecta Epizoa, p. 238) are both referable to *fusco-marginatus.* The antennal characters seem to be the same. As Piaget notes, the differing in the antennæ of male and female makes it difficult to refer the species to *Nirmus.* It is a form showing a transition to *Lipeurus.* Our specimens are one-fourth larger than the types of the species and differ in some minor particulars.

Var. *americanus* Kellogg and Chapman. (Plate V, fig. 9). Female, body, length 2.62 mm., width .81 mm.; head, length .56 mm., width .44 mm. Differs from the species type in having a spine in the posterior angles of the prothorax, and a hair on each lateral half of the posterior margin; the metathorax has six hairs and a spine on each lateral half of the posterior margin. The species is easily recognizable by its long slender body, short, narrow, pointed head, and the black, lateral, triangular, abdominal blotches with brown inward-projecting processes.

Nirmus pacificus n. sp. (Plate V, fig. 8).

Two males from a Tufted Puffin, *Lunda cirrhata;* one male from a Black-bodied Shearwater, *Puffinus griseus;* and specimens, males and females, from two Pigeon Guillemots, *Cepphus columba*—all the birds from the Bay of Monterey, California. The specimen from *Puffinus* is almost certainly a straggler, as no other specimen was taken from the fifty-five individuals of *Puffinus* examined. The new species belongs to Piaget's group *zonati* (Les Pediculines, p. 187), and is most like *citrinus* (ibid. p. 190, pl. xvi, fig. 8). The metathorax, however, is angulated, not flatly rounded, as with *citrinus*, on the abdomen, and there are other differences.

Description of the male. Body, length 1.46 mm., width .5 mm.; short, broad, Docophoroid in form; light golden brown with conspicuous broad, dark antennal bands and dark brown to black lateral abdominal bands interrupted segmentally.

Head, length .5 mm., width .4 mm.; broadly conical; clypeal front very slightly concave; three marginal hairs on the front, one on the clear portion, and two before the suture; a short marginal prickle in front of the trabeculæ, one dorsal hair just back of the first marginal, a second dorsal hair near the second marginal, two dorsal hairs between the suture and the trabeculæ which are distinct and slightly colored; the antennæ are short, segments 2 and 5 being longer than the others; color, the light golden brown of the head marked with slightly darker brown; eyes inconspicuous, with two short prickles; temples with sides nearly straight, rounding on posterior angles, with one very long hair, one shorter, weaker hair, and two short prickles; occipital margin concave; clypeus with a pale but distinct pentagonal signature; antennal bands broad and dark, continuing beyond the suture; behind the obtuse posterior angle of the signature a narrow longitudinal uncolored space extending to the mandibles; temples bordered by a very narrow line of dark brown slightly broader just below the eye; a distinct though pale occipital signature.

Prothorax quadrangular, very short, broadly rounded, angles with one rather long hair; pale medially with dark brown lateral margins that bend in along the posterior margin. Metathorax pentagonal with widely diverging sides; posterior angles acute; six hairs in the angle and along the posterior margin; the posterior margin with a distinct elongate angle on the abdomen; dark lateral markings broadest on the posterior angles. Legs pale golden brown with slightly darker marginal markings.

Abdomen slightly elongate-oval, turbinate; posterior margins of segments 1–3 angulated, and anterior margins of segments 6–9 more obtusely angled; lateral angles of segments with one to three hairs; a few hairs on dorsal surface arranged along the posterior margins of the segments; posterior margin of segment 9 broadly rounded, with ten rather long hairs, several shorter hairs on dorsal surface of segment; color of abdomen fuscous; segment 1 without distinct lateral blotches, but segments 2–7 with dark brown to black lateral blotches, darkest in anterior angles and extending along the anterior margin of each segment almost to the median line; segment 8 but little darker in anterior angle, and segment 9 of an even pale fuscous; genitalia distinctly showing through, extending to segment 6.

Female, body, length 1.75 mm., width .6 mm.; head, length .55 mm., width .47 mm.; lateral abdominal bands distinct, blackish, the posterior part of each segmental portion tapering acuminately; segment 8 without lateral bands; segment 9 widely, angularly emarginate behind, with a single very fine short hair on each obtuse posterior point.

Nirmus maritimus n. sp. (Plate VI, fig. 1.)

Many specimens from numerous individuals of the Ancient Murrelet, *Synthliboramphus antiquus*, Cassin's Auklet, *Ptychoramphus aleuticus*, Rhinoceros Auklet, *Cerorhinca monocerata.* Also a single specimen (straggler) from a Pacific Fulmar, *Fulmarus glacialis glupischa.* All of these birds from the Bay of Monterey, California. Resembling *N. citrinus* Nitzsch (Giebel, Insecta Epizoa, p. 177; Piaget, Les Pediculines, p. 190, pl. xvi, fig. 8) from *Alca torda*, but more slender, with elongate head, angulated posterior margin of metathorax, different disposition of hairs of the head, etc.

Description of the female. Body, length 1.96 mm., width .46 mm.; slender, elongate; pale fuscous with darker lateral borders on the head and thorax and broad lateral bands on the abdomen.

Head, length .5 mm., width .37 mm.; narrowly elongate, conical, with clypeal front convex; three marginal hairs, the first one near the front and the third in front of the suture, the second is midway between these; a short prickle in front of the trabeculæ which reach to the end of the first segment of the antennæ; antennæ short, not reaching more than two-thirds of the distance to the occipital margin; segment 2 longer than segment 1, and segment 5 longer than segments 3 or 4; a few short hairs on the segment; eye with a hair and a short prickle; temples with sides nearly parallel; one long hair, one short hair, and three short prickles on the margin; occipital margin slightly concave; signature distinct, shield-shaped, anterior margin convex, posterior margin produced in a narrow point; antennal bands broad, interrupted by a distinct uncolored suture; the anterior extremities of the antennal bands bend broadly in at the suture, being separated medially by a narrow uncolored line that reaches nearly if not quite to the mandibles; ocular blotch fading inwardly; temporal borders narrow but well defined, broader just below the eye, gradually narrowing till it disappears before the occipital angle; a distinct conical occipital signature showing through from the under side of the head.

Prothorax with sides slightly diverging; posterior angles rounding, with one short hair; marginal borders dark golden brown, darker on the inner margin of the border; interrupted on the posterior margin by a broad pale median line. Metathorax with broadly rounding sides, diverging posteriorly; three hairs in the posterior angles; one long and one short hair on the posterior margin each side of the long, acute, median angle; lateral margins bordered with dark golden brown, darker on the inner margin. Legs pale fuscous with narrow dark marginal bands. Sternal markings consisting of pale fuscous intercoxal markings and a distinct median sternal blotch.

Abdomen narrow, elliptical; sides of the middle segments parallel; posterior angles with from one to two hairs; four dorsal hairs on the posterior margins of the segments, two near the middle and one each side near the lateral margin; transverse bands fuscous; lateral bands deep golden brown, broader anteriorly and extending beyond the suture into the segment in front; segments 2–6 with a pale posterior border; segments

7 and 8 with pale longitudinal median band; last segment narrowly rounding, with a narrow emargination; one short hair on the posterior margin, each side of the emargination; ventral surface with broad transverse median blotches.

Male. Body, length 1.5 mm., width .4 mm.; head, length .46 mm., width .34 mm.; distinctly shorter than the female; abdomen more broadly elliptical; segments 7 and 8 narrowed distinctly in the middle; last segment broadly rounded, with ten long hairs on the posterior margin; transverse bands distinctly dark on segments 1 to 6; last segment evenly pale yellow; genitalia darker brown, extending anteriorly to segment 5.

Nirmus triangulatus Nitzsch. (Plate VI, fig. 2).

Zeitschr. f. ges. Naturwiss. (Giebel), 1866, vol. xxviii, p. 378.

Nirmus normifer Grube, v. Middendorff's Sibir. Reise, 1851, Zool. i, p. 478, pl. i, fig. 8.

Nirmus triangulatus N., Giebel, Insecta Epizoa, 1874, p. 177; Piaget, Les Pediculines, 1880, p. 201, pl. xvi, fig. 5.

Many specimens of this striking *Nirmus* from one out of two birds shot of the Pomarine Jaeger, *Stercorarius pomarinus* (Bay of Monterey, California). Our specimens differ from Piaget's figure in having the head distinctly shorter and narrower in front, giving the insect an appearance markedly different from the effect given by the figure. There is probably no doubt, however, regarding the identity of the species.

Nitzsch's specimens were taken from "*Lestris crepidata*," Grube's from "*Lestris richardsoni*," and Piaget's from *Stercorarius pomarinus* and *Larus canus* (Zool. Garden of Rotterdam).

The species may be readily recognized by the characteristic black, subtriangular, lateral, abdominal blotches, and the chestnut-brown, median, abdominal blotches (see figure). My specimens measured: Male, body, length 1.8 mm., width .62 mm.; head, length .53 mm., width .53 mm. Female, body, length 2.1 mm., width .63 mm.; head, length .6 mm., width .6 mm.

Nirmus lineolatus var. atri-marginatus. Kellogg and Chapman (For *lineolatus* see Kellogg, New Mallophaga, I, 1896, p. 113, pl. vi, figs. 7, 8 and 9).

Many specimens from *Larus canus*, *vegæ*, *brachyrhynchus* and *Rissa tridactyla pollicaris* (Bay of Monterey, California). A readily recognized variety of *lineolatus*, characterized by the presence of black temporal borders, usually strongly marked, sometimes weakly so. Other characters those of *lineolatus*.

Nirmus punctatus Nitzsch. (See Kellogg, New Mallophaga, I, 1896, p. 109, pl. vi, figs. 1 and 2).

Specimens from *Larus delewarensis* (Bay of Monterey, California). Taken previously by Kellogg from *Larus occidentalis* (same locality).

Nirmus giganticola Kellogg.

New Mallophaga, I, 1896, p. 105, pl. v, fig. 6.

Many specimens from a Short-tailed Albatross, *Diomedea albatrus*, and a single specimen from a Dark-bodied Shearwater, *Puffinus griseus* (Bay of Monterey, California). Described from *Diomedea albatrus* (same locality).

Nirmus complexivus n. sp. (Plate VI, fig. 3).

Many taken from the Sanderling, *Calidris arenaria* (Pacific Grove, California); found on every one of fifteen birds shot, and two specimens from a Least Sandpiper, *Tringa minutilla* (Palo Alto, California). This form belongs to the group *zonati*, of Piaget (Les Pediculines p. 187) and shows but slight differences from several of the species of this group already described, one or two from the same host, indeed; but on the other hand Nitzsch's and Piaget's species differ among themselves but little, and the American specimens differ quite as much from any described species. In fact they are interesting as showing a combination of several characters which are presented as diagnostic of *cingulatus* (the interrupted first abdominal band), *zonarius* (the hairs and spines of the temples, and the head longer than wide), and *scalaris* (the size). In addition they present characters (metathoracic hairs, *et al.*) which are not shown by any one of the described species. I describe the American form therefore as a new species. The group needs revision; probably four or five of the present species should be reduced to varieties of the oldest named form, i. e. *cingulatus*.

Description of the female. Body, length 1.71 mm., width .5 mm.; readily distinguishable by its general dark color, and rounding, uncolored clypeus with the distinct colored signature, on each side of which lie the narrow triangular projections of the anterior ends of the antennal bands; the posterior ends of the antennal bands bend so strongly in at the suture that they mark the fore part of the head off from the hind part into a small cone.

Head, length .4 mm., width .34 mm.; elongate, triangular, with clypeus broadly rounding, the uncolored region slightly expanded beyond the suture; two short hairs on the rounding margin of the uncolored clypeus, one rather long hair in front of the trabeculæ; trabeculæ prominent, angular, reaching beyond the first joint of the antennæ; antennæ short, reaching barely two-thirds of the distance to the occipital margin, pale fulvous with darker, broad annulations; segment 5 half as long again as segments 3 or 4; eyes distinct, with a hair and an ocular fleck; temples broadly rounding, with three long pustulated hairs, one short hair, and one prickle on the margin; occipital margin straight; clypeal signature constricted anteriorly, with the posterior, lateral angles projecting slightly backward; the posterior angle extending back indistinctly to the mandibles; antennal bands conspicuous, blackish brown, extending into long, paler, triangular projections on the clypeus; the blackish posterior ends extending in, meeting on the median line; ocular blotches contiguous with the dark temporal borders; occipital bands very definite, looking like two dark bars, bending outwards towards the ocular blotch but fading into the dark chestnut-brown of the temples; occipital blotch distinct; a pale transverse space behind the bent antennal bands, running like a curving bar across the head from margin to margin; occipital signature dark fuscous, spear-head-shaped.

Prothorax short, sides rounding; lateral quadrangular blotches separated by a narrow uncolored median line; lateral margin distinctly bordered with dark brown. Metathorax with strongly rounding sides; a short prickle in the anterior angle, a short prickle and a long pustulated hair near the middle of the lateral margin, two long pustulated hairs and two shorter hairs in the posterior angles, two short hairs on the posterior margin; the posterior margin rounding slightly upon the abdomen; strong, dark lateral bands. Legs light fulvous with dark marginal bands. Sternal markings consisting of intercoxal lines extending backward to the tip of the coxa of the second pair of legs;

a median sternal blotch rounding posteriorly with a sharp constriction about midway to the arrow-headed anterior portion.

Abdomen elongate, with one or two slender hairs in the posterior angles of the segments, two strong, pustulated hairs in the posterior margins of the segments; abdomen dark fulvous brown with broad, ill-defined, darker lateral bands, and a transverse linear band along the posterior margin of each segment of a darker brown, adjacent to which are the small uncolored stigmatal spots; the uncolored sutural lines distinct; segment 1 has the transverse band divided by a narrow uncolored median line; segments 8 and 9 more evenly colored; last segment angularly emarginated, with two anal blotches; two short hairs on the posterior margin each side of the emargination.

Nirmus actophilus n. sp. (Plate VI, fig. 4).

Many specimens from nine out of fifteen individuals shot of the Sanderling, *Calidris arenaria* (Bay of Monterey, California). A member of Piaget's group *obscuro-suturati* (Les Pediculines, p. 169) and resembling somewhat *inæqualis* (ibid., p. 176, pl. xv, fig. 1) from *Numenius arquata*.

Description of the female. Body, length 1.59 mm., width .4 mm.; pale, with distinct, narrow, lateral bands of dark brown to black, head darker brown than the thorax, with dark narrow marginal markings.

Head, length .37 mm., width .28 mm.; conical, but little wider through the temples; clypeus broadly rounded, with four marginal hairs, three on the front before the suture, and one long one before the trabeculæ, also a short prickle just at the angle of the trabeculæ; a dorsal hair between the two anterior marginal hairs, two other dorsal hairs on each side near the anterior extremity of the incurving antennal bands; trabeculæ distinct, reaching nearly to the end of the first segment of the antennæ; antennæ with segment 2 longer than segment 1, and segment 5 longer than segments 3 or 4; color pale fulvous, slightly darker on the last three segments, sutures uncolored, lateral margins slightly darker fuscous; eyes not conspicuous, flattened, with a fine hair and a short prickle; temporal margins slightly rounded, with one long weak hair, one very short hair, and three short prickles; occipital margin concave; clypeal markings distinct, marginal; signature short, distinct anterior margin fading into a broadly rounded posterior angle; behind the signature a transverse linear uncolored space, continuous with the clypeal sutures, forming a distinct uncolored transverse bar across the forehead; antennal bands well defined, bending forward at the clypeal suture into broad, quadrangular ends, posterior extremites bending backward nearly to the distinct ocular blotches, which meet posteriorly the anterior ends of the narrow black temporal borders; occipital blotches small; a distinct, elongate, oval, occipital signature showing through from the ventral side; the mandibles distinctly showing through the head, the œsophageal sclerite showing faintly.

Prothorax with flatly rounded lateral margins, each posterior angle with one pustulated hair; general color pale brown to whitish, with narrow dark lateral bands. Metathorax expanded posteriorly, angles extended, with three long pustulated hairs, and some short weak hairs in the angle and along the lateral third of the posterior margin; posterior margin slightly angulated on the abdomen; narrow black submarginal markings, broadening but less definite on the anterior angles; intercoxal lines, and a narrow, lanceolate, median, sternal blotch showing through. Legs of an even fuscous, first pair lighter than the second or third pair.

Abdomen elongate, slightly attenuated anteriorly; segments 8 and 9 tapering rapidly; posterior angles acute, each containing from one to three hairs; dorsal surface with a few hairs, four on the posterior margins of segments 1 to 7, two near the middle and two near the lateral margins; ground color pale fawn, gradually growing darker posteriorly, with dark brown lateral bands which send out from their anterior half an indefinite line that partially surrounds the stigmatal spot; segment 9 angularly emarginate, each broadly rounded angle bearing a short bristle; ventral surface with broad transverse bands of dark fawn, which give a darker tone to the paler transverse bands of the dorsal surface; a more definite series of hairs on the posterior margin of the segments than above; segment 8 with a group of three short hairs near the lateral margin.

Nirmus cordatus Osborn.

Insects Affecting Domestic Animals, Bull. 5, N. S., Div. of Ent., U. S. Dept. Ag., 1896, p. 228, pl. ii, fig. *a*.

One female specimen from a Great Marbled Godwit, *Limosa fedoa* (Pacific Grove, California). We had determined this to be an undescribed form, and had partially written a description when Professor Osborn's paper appeared, naming and describing the species from a single female and an immature specimen from the Hudsonian Godwit, *Limosa hæmastica* (Burnett Collection, locality?). Our specimen agrees well with Osborn's description, except that it is somewhat larger, being 2.75 mm., long (Osborn's type 2.44 mm.), and 1.2

mm. wide, (Osborn's type .94 mm.); head, length .7 mm., (Osborn, .66 mm.), width .85 mm., (Osborn, .73 mm.) Osborn's figure, after a photograph, shows the characteristic outline, but we think there is also needed a figure showing the markings which are also very characteristic. The broad rounding anterior emarginations of first two transverse abdominal bands differ notably from the not uncommon narrow angular emarginations of these bands.

Nirmus incœnis n. sp. (Plate VI, fig. 5).

A single female from a Black-bellied Plover, *Squatarola squatarola* (Pacific Grove, California). Distinctly different from Kellogg's *orarius* (New Mallophaga I, 1896, p. 104, pl. v, fig. 5) from *Charadrius dominicus* (Lawrence, Kansas) or *bœphilus* (ibid, p. 107, pl. v, fig. 7) from *Ægialitis vocifera* (Lawrence, Kansas).

Description of the female. Body, length 1.65 mm., width .31 mm.; strikingly elongate, narrow; head long, with subparallel sides; pale golden brown with very narrow blackish lateral borders on the head, thorax, and abdomen; an ill-defined brownish band across the head in front of the antennal bands.

Head, length .37 mm., width .21 mm.; clypeal front broadly rounding, with three marginal hairs about equally distant apart, the third just before the suture, one hair arising from the dorsal surface, extending beyond the lateral margin of the head, a short fine hair in front of the small acuminate trabeculæ, antennæ short, segment 2 longer than segment 1, and segment 5 longer than segments 3 or 4; eye flat, with a prickle near its posterior angle; temples with sides parallel, with one long hair, one short fine hair, and one short prickle on the margin; occipital margin straight and bare; general color of the head golden brown, a narrow, irregular, marginal border on the clypeal front, darker on the inner margin; a weak brown band across the head in front of the antennal bands, which are narrow and distinctly dark golden brown; small ocular blotches and temples with very narrow dark brown borders.

Prothorax quadrangular, with rounding, posterior angles, each with one hair; transverse blotches golden brown, darker on the lateral margins and in the anterior and posterior angles; a broad, pale, median line separating the transverse blotches. Metathorax more than twice as long as the prothorax, and as wide as the head; sides diverging but little; a slight constriction near the anterior angles; a series of hairs on the rounding posterior margin; same golden brown as the prothorax, a narrow marginal border and a small brown spot in the anterior angles, a narrow but well defined border on the posterior half of the metathorax, the anterior ends bending in, making the slight constriction appear more than it really is. Legs paler golden brown than the thorax, with very narrow marginal borders of dark brown.

Abdomen narrow, elongate, with parallel sides, not tapering till segment 7; segment 1 narrower and shorter than those that follow; posterior angles but little extended, with one or two fine hairs; four long pustulated hairs on the posterior margins of the segments; transverse bands on segments 2 to 8 are golden brown, darkening towards the lateral margins where the lateral band is dark, narrow, and clearly defined; segments 7 to 9 without lateral bands; a pale transverse median band, caused by the uncolored stigmatal spots, thus the transverse blotches appear like two dark bands across each segment; segment 9 narrowly emarginate, with two pale brown blotches.

Nirmus opacus n. sp. (Plate VI, fig. 6).

Several specimens from two individuals of the Semipalmated Plover, *Ægialitis semipalmata* (Pacific Grove, California). The new species belongs to the group *bicuspidati* (Piaget, Les Pediculines, p. 184), being in size, outline and marking much like *bicuspis* N. (Giebel, Insecta Epizoa, p. 155, pl. v, figs. 11 and 12; Piaget, Les Pediculines, p. 184, pl. xv, fig. 7) from "*Charadrius minor*," *C. hiaticula* and *Recurvirostra avocetta.*

Description of the male. Body, length 1.11 mm., width .47 mm.; body dark colored all over, with narrow black lateral abdominal bands.

Head, length .4 mm., width .31 mm.; elongate-conical, with broad, rounding front; uncolored clypeal region slightly expanded in front of the suture; five marginal hairs, one in the rounding anterior angle, one just behind this, one at the suture, and two before the trabeculæ; a few dorsal hairs project beyond the margin; trabeculæ distinct, rather slender, acute, prominent for *Nirmus;* antennæ short, not reaching the occipital margin when projected backward, segment 2 longest, segments 3 and 4 short, subequal, segment 5 longer, concolorous with ground color of the head; eyes flat, with a long hair and a fine prickle; temporal margins flatly rounding, with two long hairs and two prickles; occipital margin straight; front of clypeus uncolored; signature large, colored, shield-shaped, from its posterior point a narrow uncolored line runs backward to the mandibles or beyond; antennal bands distinct, blackish brown, interrupted at suture, the part behind the suture curving, with anterior extremity expanded; hind head separated from fore head by an angulated, rather broad pale transveral space; temples unevenly bordered with blackish brown.

Prothorax quadrangular, with posterior angles nearly rectangular, with one long hair; brown with blackish, even, lateral borders. Metathorax pentagonal, angulated on abdomen; lateral angles with one short hair and three long pustulated hairs, and two long pustulated and one short pustulated on each postero-lateral margin; brown, darker in anterior angles. Legs concolorous with palest color of the thorax, and with narrow dark dorsal margining. Sternal markings composed of distinct intercoxal lines, a linear median blotch on prothorax and a more distinct, larger median blotch on metathorax.

Abdomen elongate-elliptical; posterior angles of segments projecting slightly, with three or four longish hairs beginning with segment 3; dorsal hairs of segment 1 arranged as follows: two on each side of the median line (one in the inner anterior and one in the inner posterior angle of each lateral blotch); segment 2 with four pustulated hairs along the posterior margin; segments 3 and 4 with six pustulated hairs on posterior margin; segments 5 and 6 with two pustulated hairs near the middle of the posterior margin, and a very long hair on the posterior margin near the posterior angles; segment 8 with six pustulated hairs along the posterior margin; segment 9 with eight dorsal hairs and four long marginal hairs; dark brown, with distinct narrow black lateral bands; a narrow uncolored median line reaching nearly to posterior margin of segment 2; the dark brown transverse blotches on segments 6–8 broadly emarginated posteriorly; segment 9 with elongate-elliptical transverse lateral blotches meeting on the median line (there are four pustulated hairs on each blotch); genitalia distinct, extending to posterior margin of segment 4.

Female. Body, length 1.75 mm., width .45 mm.; head, length .47 mm., width .28 mm. Metathorax with but two pustulated hairs on each postero-lateral margin; the narrow uncolored median line extends entirely through segment 2, and slightly into segment 3; segments 3–6 with four pustulated hairs on posterior margin, segment 7 with two median pustulated hairs on posterior margin, and segment 8 with two pustulated hairs in the rounding posterior angles; segment 9 deeply, angularly emarginated, the acute joints with a short prickle.

Nirmus fuscus Nitzsch. (See Kellogg, New Mallophaga, II, 1896, p. 499, pl. lxvii, fig. 7).

Specimens from the Western Goshawk, *Accipiter atricapillus striatulus* (Pullman, Washington), the Desert Sparrow Hawk, *Falco sparverius deserticolus* (Palo Alto, California), the Western Red-tailed Hawk, *Buteo borealis calurus* (Palo Alto, California), and the White-tailed Kite, *Elanus leucurus* (Palo Alto, California). Taken previously by Kellogg from *Buteo swainsoni*, *Circus hudsonius* and *Archibuteo lagopus sancti-johannis*, all from Lawrence, Kansas. Recorded by Osborn from *Buteo swainsoni* (Ames, Iowa), and from *Accipiter velox* (locality ?).

These specimens combine characters of *fuscus*, *rufus*, *et al.* of Nitzsch, so as to lead us to doubt the distinctness of these various species of Nitzsch. We have with *Nirmus fuscus*, *sens latus*, of the hawks, a repetition of the condition shown by *Docophorus communis* of the passerine birds.

Nirmus vulgatus Kellogg.

New Mallophaga, II, 1896, p. 496, pl. lxvii, fig. 5.

Many specimens from numerous species of passerine birds. This *Nirmus* must be treated like *Docophorus communis*, in that we must group together under one specific name forms rather variant (notably in length and intensity of coloration), without being able as yet to distinguish categorically these variations. Osborn's *pallidus* (Insects Affecting Domestic Animals, 1896, Bull. 5, N. S., Div. of Ent., U. S. Dept. Ag., p. 227). from *Zamelodia ludoviciana* (Ames, Iowa) is probably based on palely colored specimens of this species. The name *N. pallidus*, by the way, is preoccupied (see Piaget, Les Pediculines, 1880, p. 144).

We refer to this species specimens from the Western Blue Grosbeak, *Guiraca cærulea eurhyncha* (4 birds, California); the Western Lark Sparrow, *Chondestes grammacus strigatus* (Ontario, California); the House Finch, *Carpodacus mexicanus frontalis* (Ontario, California); the California Towhee, *Pipilo fuscus crissalis* (2 birds, Palo Alto, California); the Spurred Towhee, *Pipilo maculatus megalonyx* (Palo Alto, California); the Golden-crowned Sparrow, *Zonotrichia coronata* (Palo, Alto, California); the Lazuli Bunting, *Passerina amœna* (Palo Alto, California); the Mountain Chickadee, *Parus gambeli* (El Dorado county, California); the Californian Chickadee, *Parus rufescens neglectus* (Palo Alto, California); the Western Bluebird, *Sialia mexicana occidentalis* (Palo Alto, California); the Yellow Warbler, *Dendroica æstiva* (Palo Alto, California); the Lutescent Warbler, *Helminthophila celata lutescens* (Palo Alto, California); the Black-chinned Hummingbird, *Trochilus alexandri* (Ontario, California); the Blue-fronted Jay, *Cyanocitta stelleri frontalis* (King's River

Cañon, California); the American Dipper, *Cinclus mexicanus* (Ontario, California); the Western Flycatcher, *Empidonax difficilis* (2 birds, Ontario, California), and the Ash-throated Flycatcher, *Myiarchus cinerascens* (Ontario, California). The specimens from the two last-named bird species, Flycatchers, show a common variation from the type specimens in a greater length, less angulated posterior margin of metathorax, and paler markings. Taken previously by Kellogg from eight species of passerine birds.

Nirmus fœdus n. sp. (Plate VI, fig. 7).

Specimens from the Ash-throated Flycatcher, *Myiarchus cinerascens* (Ontario, California), the Long-tailed Chat, *Icteria virens longicauda* (Ontario, California), Say's Phœbe, *Sayornis saya* (Ontario, California), the Arkansas King-bird, *Tyrannus verticalis* (Ontario, California), the California Shrike, *Lanius ludovicianus gambeli* (Ontario, California) and the Phainopepla, *Phainopepla nitens* (Ontario, California). This species belongs to Piaget's second group of *circumfasciati*, and resembles *platyclypeatus* P. and *frater* (Les Pediculines, p. 145, pl. xii, figs. 1 and 2) from *Motacilla alba* and *Lamprotornis amethystina*, respectively.

Description of the female. Body, length 2.21 mm., width .75 mm.; abdomen broad for *Nirmus*, pale fuscous, head darker than the thorax or abdomen, narrow dark lateral borders on the head and thorax, but no dark lateral abdominal bands; pale brown median, transverse abdominal blotches.

Head, length .56 mm., width .43 mm.; clypeal front varying from narrowly to broadly parabolic, with four short hairs on the margin, a short marginal prickle before the trabeculæ, and two long dorsal hairs arising before the trabeculæ, which are small, yet distinct; antennæ short, segment 2 longer than the other segments, segment 5 longer than segments 3 or 4, a few short hairs on the segments; eye distinct, with one very long hair and a short prickle at its posterior angle; temples rounded, with two long marginal hairs and two or three short prickles; occipital margin straight; head of a general dark fulvous, clypeal front paler, clearer yellow brown; antennal bands very narrow, blackish brown, strictly marginal and not extending far anteriorly; antennæ an even, pale fuscous; ocular blotches dark and extending angularly inward; temples with a narrow border of blackish brown.

Prothorax with sides rounding and slightly divergent, with a long hair in the posterior angle; three short dorsal spines near the anterior angle, two near the median line, and one nearer the lateral margin; lateral margins with irregular dark borders; intercoxal lines showing through from the under side distinctly, as sharply defined lines, directed in towards the median line, before the posterior margin. Metathorax but little wider than the prothorax, slightly constricted near the anterior angles; posterior angles broadly rounded, with one short hair and one spine; posterior margins nearly straight on the abdomen, except for the acute median angle; a series of long pustulated hairs on the posterior margin each side of the acute angle. Legs pale fuscous without definite markings.

Abdomen broadly elliptical; angles of segments not projecting, a series of long hairs on the posterior margin of the segments; transverse bands an even, pale fuscous, indistinct to wanting, without darker lateral bands; last segment broadly rounding, with slight emargination, two or three short marginal hairs and several long dorsal hairs; ventral surface with broad median transverse bands of dark fuscous; blotches of the last segment posteriorly emarginate and laterally interrupted by the pustulations of two long hairs; these ventral blotches show through above.

Nirmus ductilis n. sp. (Plate VI, fig. 8).

One female from a Western Flycatcher, *Empidonax difficilis* (Ontario, California). A member of the group *interrupto-fasciati*, but well distinguished by its sharp, distinct, blackish marginal markings, without trace of median abdominal blotches.

Description of the female. Body, length 1.9 mm., width .4 mm.; long, slender, transparent white, with narrow, distinct, blackish lateral margins of head and abdomen.

Head, length .37 mm., width .28 mm.; elongate, conical, front narrow and slightly concave; a few short hairs along the margin of the front, the longest hair in front of the trabeculæ, which are small but distinct and uncolored; antennæ with second segment longest, segment 5 longer than segments 3 or 4, segments 1 and 2 pale transparent whitish, segment 3 with a slight shade of brown, segments 4 and 5 dark brown; eye with a prickle; temporal margins with one long hair and two or three prickles; occipital margin slightly convex; antennal bands narrow, blackish brown, fading out along the inner margins and anteriorly, before reaching the uncolored frontal margin, the posterior extremities bending angularly in, meeting the dark ocular blotches which in turn meet the dark brown marginal borders of the temples.

Prothorax with flatly rounding lateral margins and posterior angles, dark blackish brown lateral borders, which bend in and back on the anterior and posterior extremities, the posterior borders almost meeting on the median line. Metathorax as wide as the head, sides diverging strongly; posterior angles with three or four long hairs, a series of pustulated hairs along the outer third of the posterior margin that is rounded upon the abdomen; dark, interrupted lateral blotches narrow and marginal on the anterior angles, and large, irregular submarginal blotches, darker near the posterior angles, growing paler near the middle. Sternal markings consisting of distinct intercoxal lines and a pale brown median blotch on the metasternum. Legs translucent whitish with blackish brown marginal bands and semi-annulations.

Abdomen very long, elliptical, with subparallel sides not tapering posteriorly until after segment 7; posterior angles of the segments slightly projecting, each bearing one weak hair, till segment 7, which has two hairs in the angle; segment 8 has one lateral marginal hair besides two hairs in the posterior angle; segment 9 broadly rounding, with angular emarginations, two short hairs on the posterior margin; two dorsal hairs arising near the posterior angle of each segment except segment 8 which has a series of posterior marginal hairs; pale translucent whitish with distinct, narrow blackish brown linear bands on the lateral margins of segments 1 to 7; segment 8 with small pale brown blotches near the lateral margin and one pale brown blotch on the median line; last segment uncolored; genital blotches pale brown, linear each side of the median line on the posterior margin of segment 7, also a pale brown blotch on the median line of segment 6.

Nirmus lautiusculus n. sp. (Plate VI, fig. 9).

A single male from a Bell's Sparrow, *Amphispiza belli* (Ontario, California). The new species, strikingly marked, is a member of the group *interrupto-fasciati*, in general shape like *vulgatus* K. (New Mallophaga II, p. 496, pl. lxvii, fig. 5) and with the characteristic angulated, colored internal border of the antennal fossa. In the distinctness and contrast of the markings it recalls *illustris* K. (New Mallophaga II, p. 494, pl. lxvii, fig. 4).

Description of the male. Body, length 1.65 mm., width .4 mm.; translucent whitish with sharp, black, narrow marginal bands on head and abdomen; legs with annulations and semiannulations; thorax with intercoxal lines showing through distinctly, and abdomen with median linear brown transverse blotches, two to a segment, on ventral aspect.

Head, length .34 mm., width .31 mm.; front narrow, slightly convex; two or three short hairs on the lateral margin of the front; a short prickle in front of the trabeculæ which are distinctly angular and uncolored; antennæ long; segment 2 longer than other segments, segment 5 distinctly dark brown; eye prominent, with two prickles, one on the eye itself and a second just at its posterior angle; temples rounding, with one very long hair, one short fine hair, and three short prickles; occipital margin straight and bare; antennal bands narrow, clearly defined, not fading inwardly, their anterior extremities separated by the uncolored clypeal front, interrupted just before the trabeculæ by a distinct uncolored space, posterior extremities acutely meeting the dark narrow bands that angularly margin the antennary fossæ and the eye; the temples irregularly dark on the margins; the occipital signature distinctly showing through as a narrow brown blotch on the occipital margin and in front as a triangular blotch.

Prothorax with rounding lateral margins and posterior angles; three short spines on the dorsal surface in each anterior angle; a dark blackish brown blotch in the anterior angles, and a narrow black band along the posterior margin, widening as it reaches the angle. Metathorax longer than the prothorax, with sides diverging; a series of six long hairs on the posterior margin which is narrowly rounded upon the abdomen; anterior angles with a small blotch of dark brown. Sternal markings showing through distinctly, the intercoxal lines of the metasternum appearing as a dark transverse band across the metathorax, the lateral extremities not reaching the margin but bending irregularly backward, abruptly stopping before they reach the posterior angle. Legs translucent with dark annulations and semiannulations.

Abdomen narrowly elongate, segments 1–7 with narrow, sharply defined black lateral bands; last segment uncolored, narrowly rounding, with several long dorsal hairs; the ventral surface of segments 1–6 with two median, linear brown transverse blotches on each segment; these blotches are united on segment 6 by a brown median line; segment 7 with two longitudinal brown blotches each side of the median line approaching each other anteriorly; two very small brown blotches on the last segment near the anterior angle.

Nirmus longus Kellogg.

New Mallophaga, II, 1896, p. 490, pl. lxvii, fig. 1.

A single male from the Barn Swallow, *Chelidon erythrogastra* (Palo Alto ? California). This specimen differs distinctly from the type specimens in having but three instead of six lateral metathoracic hairs, in the more elongate head, and in the distinctness of the median uncolored longitudinal line of the abdomen. It should be distinguished by a varietal name.

Var. *domesticus* Kellogg and Chapman; one male from the Barn Swallow, *Chelidon erythrogastra* (California); body, length 1.54 mm., width .41 mm; head, length .37 mm., width .31 mm.; thus being of about same size as the species type, and twice as long as Nitzsch's *gracilis*, the common *Nirmus* of the European swallows. Characters of species with differences as noted above. Osborn (Insects Affecting Domestic Animals, 1896, p. 225) refers a specimen from the Purple Martin, *Progne subis* (Ames, Iowa), to *gracilis*. He does not give the measurements of his specimen.

Nirmus brachythorax Giebel.

Insecta Epizoa, 1874, p. 134.

Nirmus brachythorax G., Piaget, Les Pediculines, 1880, p. 150, pl. xii, fig. 8; Osborn, Insects Affecting Domestic Animals, Bull. 5, N. S., Div. of Ent., U. S. Dept. Ag., 1896, p. 223.

Specimens from two Cedar Waxwings, *Ampelis cedrorum* (Palo Alto, California). Osborn's specimens were from same host (Ames, Iowa). Giebel's types are from same host.

Lipeurus.

Lipeurus laculatus n. sp. (Plate VII, fig. 1).

Four specimens collected of this strikingly marked *Lipeurus;* an adult male and an immature individual from a Pomarine Jaeger, *Stercorarius pomarinus*, and an adult male and an immature from a Pink-footed Shearwater, *Puffinus creatopus* (Bay of Monterey, Calif.) We believe that the specimens from the Shearwaters are stragglers from the Jaeger. (We have examined so many Shearwaters that, were the species a regular parasite of *Puffinus*, we should have taken other examples.) One other individual of *Stercorarius pomarinus* was examined, but no *Lipeurus* was found on it. The new species shows no special resemblances to any of the described *Lipeuri* of allied hosts.

Female. Body, length 4.06 mm., width .78 mm.; slender, transparent whitish with distinct black marginal markings on the head, thorax, legs, and abdomen, broad transverse bands of dark chestnut showing through the dorsal surface of the abdomen.

Head, length 1. mm., width .59 mm.; elongate, conical, sides nearly parallel, clypeal front rather narrowly rounded, with five marginal hairs, four of which arise from the anterior part of the clypeus, being about equidistant, the fifth hair is in front of the very small trabeculæ; two dorsolateral hairs, one near the first anterior marginal hair and the other between the third and fourth marginal hairs; antennæ with segment 2 longer than the other segments, segments 1, 2 and 3 uncolored, segment 4 dark brown, segment 5 lighter brown; eye distinct, with a short prickle; temporal margins nearly parallel, with one hair and four short prickles; anterior margin of the clypeus uncolored; a wide, distinct signature with convex, posterior margin; color even chestnut-brown; antennal bands broad, black, sharply defined, except at the anterior portion where they extend indistinctly toward the median line of the head; temporal margin distinctly bordered with black, narrowing posteriorly; occipital blotches black and angular.

Prothorax quadrangular, sides parallel; a short prickle in the posterior angles; pale transparent brown, with broad black lateral borders following the margins of the anterior and posterior angles. Metathorax longer than broad, widest at the posterior angles; posterior margin straight; ground color slightly darker brown than the prothorax, with irregular, black marginal bands fading just back of the anterior angles, and with an emargination at their posterior extremity where four long pustulated hairs and one short hair arise; one short hair on the posterior angle. Legs concolorous with the pale color of the prothorax, with black annulations and marginal bands; front legs short, femora wide, with small black marginal markings; second and third pair of legs long; coxæ produced and widely separated, with dark dorsal annulations; femora long and slender, with narrow black marginal markings; tarsi and claws pale brown; several scattered hairs and spines on the legs. Sternal markings composed of intercoxal lines between pro- and mesolegs, and a large suboblong, metathoracic, median blotch with rounded angles.

Abdomen with sides of segments 1–7 parallel; segments 8 and 9 suddenly narrowed and very small; posterior angles of the segments with from one to four long hairs; segment 9 narrowly emarginate, with two long hairs on each of the posterior angles; ground color transparent whitish, with black lateral marginal bands which extend inward along the anterior and posterior margins; these lateral bands are inwardly emarginated by an uncolored space surrounding the stigmata; on the ventral aspect fulvous transverse bands, concave posteriorly; segment 7 with two longitudinal, lateral fulvous blotches; segment 8 with irregular black marginal bands; segment 9 wholly dark brown to black.

Lipeurus diversus Kellogg.

New Mallophaga I, 1896, p. 123, pl. viii, figs. 3 and 4.

Many specimens from thirteen out of thirty-four individuals shot of the Black-vented Shearwater, *Puffinus* *opisthomelas*, from twelve out of fourteen individuals shot of the Dark-bodied Shearwater, *P. griseus*, from five out of six individuals shot of the Pink-footed Shearwater, *P. creatopus*, from a single specimen shot of *P. bulleri*, from a single specimen shot of *P. tenuirostris*, and a single specimen, probably straggler, from a Short-tailed Albatross, *Diomedea albatrus* (all the birds from the Bay of Monterey, California). The species was described from *Puffinus opisthomelas* (same locality).

This species and *Lipeurus angusticeps* Piaget (Les Pediculines, p. 306, pl. xxv, fig. 4) from *Thalassidroma leachi*, and *Lipeurus abnormis* Piaget (Supplement, p. 65, pl. vii, fig. 2) from *Puffinus major*, are closely related. There is a regular sequence in size from *angusticeps* through *diversus* to *abnormis*. It may be suspected that we have to do with one species of great variation in size; but the diagnostic characters of the three species are sufficiently important to justify the separation of the forms.

Lipeurus densus Kellogg.

New Mallophaga II, 1896, p. 114, pl. vii, figs. 1 and 2.

Two females and a male from a Short-tailed Albatross, *Diomedea albatrus* (Bay of Monterey, California). Types taken from *Diomedea albatrus* and *D. nigripes* (see Kellogg, Mallophaga from Birds of Panama, Baja California and Alaska, in New Mallophaga III, p. 28, pl. iii, fig. 2). These specimens fully confirm the specific idendity of the female described in New Mallophaga II, p. 114, and the male described in New Mallophaga, III, p. 28. The females now taken are almost, if not quite, as large as the male, and they are also quite as fully blotched and colored.

Lipeurus ferox Giebel. (See Kellogg, New Mallophaga, I, 1896, p. 127, pl. ix, figs. 1 and 2).

One male from the Short-tailed Albatross, *Diomedea albatrus* (Bay of Monterey, California). Previously taken by Kellogg from same host species (same locality). The description and figure which Taschenberg (Die Mallophagen, 1882, p. 145, pl. v, fig. 1 *a*) gives for the female of *Lipeurus ferox* apply in reality, we believe, to the male of *Lipeurus densus* Kellogg (See Mallophaga from Birds of Panama, Baja California and Alaska, in New Mallophaga, III, 1899, p. 28, pl. iii, fig. 2).

Lipeurus concinnus n. sp. (Plate VII, fig. 2).

A male and a female from the Short-tailed Albatross, *Diomedea albatrus* (Bay of Monterey, California). A slender, graceful form of the *clypeati sutura indistincta*, not much resembling any of the *Lipeuri* hitherto taken on the Albatross.

Description of the male. Body, length 3. mm., width .53 mm.; slender, pale, with distinct black marginal markings, and brown head and transverse abdominal blotches.

Head, length .65 mm., width .4 mm.; elongate, conical, front rounded, four long marginal hairs and one short one before the antennal angle; a long hair, arising from the dorsal surface between the first and second marginal hairs, extends beyond the margin; antennæ with segment 1 nearly as long as all the other segments, segment 2 about one-third as long as segment 1, segment 3 short, with a dorsal, angular, distal appendage, segment 5 longer than segment 4, segments 4 and 5 and the tip of the appendage of segment 3 light brown, antennæ elsewhere uncolored; eyes distinct but not protruding; temples convex, hind-head widest about half way between the eyes and the posterior angles; margin with no long hairs, but with a short curving hair and a few prickles; occipital margin straight; head all brown, except small, nearly uncolored part of clypeal front, and antennæ, of which the first three segments are uncolored, last two pale brown; narrow marginal antennal bands; small signature, widest anteriorly and extending posteriorly in a fading, acuminate point; indistinct occipital bands and temporal borders blackish; anterior horns of the prothorax showing through, producing the effect of black triangular blotches at the base of the occipital bands.

Prothorax quadrangular, straight in the middle third on the metathorax; one very short hair in the posterior angle; general color transparent whitish, with distinct, even black lateral borders. Metathorax with lateral margins slightly convex before the middle; longer than broad; posterior margin slightly angulated upon the abdomen; three long hairs and two shorter hairs in the posterior angles; general color pale transparent brownish, with irregular lateral bands of black, expanding near the anterior angles into conspicuous triangular blotches, narrower below these blotches than the lateral bands of the prothorax. Legs long, slender, transparent, with black bands on femora and tibiæ; tibiæ and tarsi brown, a few scattered hairs on the legs. Prosternum with curving intercoxal lines; a medial, metathoracic, sternal blotch oblong, darker on the posterior half.

Abdomen slender, elongate, slightly widening to segment 4, then tapering gradually to segment 9; segment 2 longer than the other segments, while segments 4 and 5 are narrow, especially in the middle; posterior angles but slightly extending, with from one to four hairs; segment 8 with six long posterior marginal hairs; general ground color of the abdomen, after segment 1, which is transparent whitish, dark brown; lateral markings black, of segment 1 they are anterior and angular, of segments 2 to 7 broadly extending towards the median line on the anterior half of the segments, while the posterior portion is darker and more definitely angular, this lateral band is deeply emarginated interiorly by a light brown blotch; the broad transverse bands are darker on the anterior margin, and the posterior margins of these transverse bands are emarginated by a pale brown band; segment 8 an even brown with very narrow dark lateral bands; segment 9 very small, rounding, of an even brown, with two long and two short hairs on the posterior margin.

Female. Body, length 3.63 mm., width .68 mm.; head, length .68 mm., width .43 mm.; first and second segments of antennæ nearly equal and as long as the other three segments, segment 5 longer than segment 4, segments 4 and 5 slightly colored with brown; eyes larger and more prominent than in the male; segments of the abdomen more nearly equal than in the male; segments 8 and 9 suddenly narrower than segment 7; segment 8 with a strong conspicuous hair in each anterior angle; six hairs along the posterior margin and eight small hairs in a transverse curving line on the ventral aspect; segment 9 with one hair in each anterior angle and two strong hairs on each of the two obtuse points, separated by the angular emargination of the posterior margin. Abdominal markings limited to dark brown to black, lateral blotches with pale, indistinct stigmatal spots; segments 7 to 9 almost wholly brown, with a narrow, distinct, uncolored median line; lateral parts of segment 7 blackish brown.

Lipeurus testaceous Taschenberg. (See Kellogg, New Mallophaga, I, 1896, p. 130, pl. xi, figs. 2 and 4).

A few specimens, rarely more than one or two from a bird, from eight out of thirty-four individuals shot of the Black-vented Shearwater, *Puffinus opisthomelas;* not found on any one of fourteen individuals shot of *P. griseus;* found on one out of six individuals shot of *P. creatopus;* and not found on the single specimen examined of *P. bulleri*, nor of *P. tenuirostris*, all from the Bay of Monterey, Calif. Taken previously by Kellogg from *Puffinus opisthomelas*, same locality. We have no males among the few specimens collected.

Lipeurus limitatus Kellogg.

New Mallophaga, I, 1896, p. 124, pl. viii, figs. 5 and 6.

Many specimens from five out of thirty-four individuals shot of the Black-vented Shearwater, *Puffinus opisthomelas;* from five out of fourteen individuals shot of *P. griseus;* from none out of six individuals shot of *P. creatopus;* from a single individual shot of *P. bulleri*, and from a single individual shot of *P. tenuirostris*, all from the Bay of Monterey, California. Described from three females from *P. griseus*, same locality. We are unable to find any males among our rather many specimens.

Lipeurus fuliginosus Taschenberg. (Plate VII, fig. 3).

Die Mallophagen, 1882, p. 156, pl. iv, fig. 3.

Numerous examples from the Shearwaters, *Puffinus opisthomelas* and *creatopus* (Bay of Monterey, California). Taken from eight out of thirty-four birds shot of *opisthomelas*, from one out of six birds shot of *creatopus*, and not found on any one of fourteen birds shot of *griseus*. The American specimens differ from the types of *fuliginosus*, which were collected from *Diomedea exulans* and *chlororhyncha* by being larger, by showing no difference in the clypeal front of male and female, by having no short hair in the eye, and in other minor characters. We make a variety, therefore, for them.

Var. *major* Kellogg and Chapman. (Plate VII, fig. 3). In the following table of dimensions the figures enclosed in parentheses are the measurements given by Taschenberg for the type specimens. Male. Body, length 3.75 mm. (3.32 mm.), width .9 mm. (.58 mm.); head, length 1. mm. (.89 mm.), width .66 mm. (.55 mm.) Female. Body, length 3.9 mm. (3.72 mm.), width .94 mm. (.66 mm.); head, 1.05 mm. (.9 mm.), width .7 mm. (.59 mm.). From these measurements the head of the variety is proportionately wider than in the type forms. The species is recognizable by its dark color and the characteristic double set of internal bands in the forehead.

Lipeurus farallonii Kellogg. (Plate VII, fig. 4).

New Mallophaga, I, 1896, p. 103, pl. v, fig. 4.

Many specimes from two individuals of Brandt's Cormorant, *Phalacrocorax penicillatus* (Bay of Monterey, California). Described (as a *Nirmus*) from a single female from a Farallon Cormorant, *Phalacrocorax dilophus albociliatus* (Bay of Monterey, California). The finding of the males of this species shows that it is a *Lipeurus* of the group *clypeati sutura distincta* and allied to Piaget's *setosus*, *sub-setosus*, *et al.* taken from various cormorants. The marked difference in size, outline and marking of the two sexes is striking, and likely to be confusing to students who may happen to meet but one sex. Is it possible that Piaget's *Nirmus dispar*, which the female of *farallonii* resembles, can be the female of some one of these *Lipeuri* of the cormorants?

Description of the male. Body, length 1.72 mm., width .36 mm.; head, length .43 mm., width .37 mm.; head like female, perhaps a little narrower, comparatively, behind; antennæ with segments 1 and 2 rather large, subequal, segments 3 and 4 very small, subequal, and segment 5 as long as 3 and 4 together, no distinct appendage; metathorax with sides nearly parallel, not plainly divergent as in female; abdomen slender, sides subparallel, ground color pale golden with wide whitish transverse sutural bands and prominent brown, shining subcircular lateral blotches not touching the narrow, inconspicuous blackish lateral bands; last segment truncate behind, with a group of four prominent hairs on each lateral half of the margin.

Lipeurus forficulatus Nitzsch. (See Kellogg, New Mallophaga, I, 1896, p. 129, pl. ix, figs. 3, 4, 5 and 6).

Specimens from a Californian Brown Pelican, *Pelecanus californicus* (Bay of Monterey, California). Taken previously by Kellogg from same host species, same locality; and from the White Pelican, *P. erythrorhynchus* (Lawrence, Kansas.)

Lipeurus squalidus Nitzsch. (See Kellogg, New Mallophaga, I, 1896, p. 132, pl. x, figs. 6 and 7.)

Six specimens from a Shoveller, *Spatula clypeata* (Palo Alto, California). These specimens resemble very much those specimens which Kellogg collected from *Merganser serrator* (see New Mallophaga, I, p. 130, pl. x, fig. 1). In fact, we fail to make out any good distinction between the species *temporalis* Nitzsch (found on the Mergansers) and the species *squalidus* of *Anas* and allied ducks.

Lipeurus docophoroides Piaget. (See Kellogg, New Mallophaga, II, 1896, pl. lxviii, fig. 8).

Two female specimens from a Plumed Partridge, *Oreortyx pictus plumiferus* (El Dorado county, California). These specimens differ distinctly in the less pointed front from *L. docophoroides* taken by Kellogg from *Callipepla californica*, and in this form a link between *docophoroides* and *dissimilis* Piaget (see Kellogg, New Mallophaga, II, 1896, p. 507, pl. lxviii, fig. 7). We have given these specimens a varietal name.

Var. *californicus* Kellogg and Chapman, from the Plumed Partridge, *Oreortyx pictus plumiferus* (El Dorado county, California); clypeal front not so pointed as in the species type, but approaching the rounded front of *dissimilis* P.; without signature; all the antennal segments colored, at least slightly, instead of only the last three as in the species type; the pustulated hairs of the body very long (longer than in the typical species forms).

Lipeurus perplexus n. sp. (Plate VII, fig. 5).

Two females from a Columbian Sharp-tailed Grouse, *Pediocætes phasianellus columbianus* (Pullman, Washington), and many females, differing slightly in shape of metathorax and abdomen, from a Sooty Grouse, *Dendragapus obscurus fuliginosus* (Kings River Cañon, California). A peculiar broad, robust form of the group *circumfasciati*, with rounded front. Resembling Piaget's *L. opimus* (Supplement, p. 78, pl. viii, fig. 6) from *Turacus giganteus* (Museum of Leyden). Resembling also in general outline and characters Osborn's *Nirmus cordatus*, a specimen of which we have taken from *Limosa hæmastica*. Perhaps both of these forms should be referred to the same genus. Piaget's *L. opimus* should accompany them. Unfortunately, all of these species are represented by females only.

Description of female. Body, length 2.06 mm., width .59 mm.; short, broadly elliptical body, with short, broad head, broadly rounded in front; clear fulvous with pale golden brown lateral, transverse abdominal blotches.

Head, length .53 mm.; width .5 mm.; cordate, clypeal front broadly rounded, four short marginal hairs on the front, a short hair on the margin in front of the antennæ which are short; segment 2 of the antennæ longer than segment 1, segment 5 longer than segments 3 or 4; the anterior end of segment 3 and segments 4 and 5 pale fulvous, a few short hairs on the segments; eye prominent, a long hair rising from its dorsal surface, and with a conspicuous black fleck; temples convex, with two long hairs and two or three short prickles; occipital margin slightly concave; antennal bands slightly darker on the posterior tips and continuous as a narrow, even marginal border of pale translucent golden brown on the front; narrow, occipital blotch of pale golden brown, also a temporal border and an occipital band of the same color; mandibles dark chestnut-brown, showing through the head.

Prothorax short, lateral margins convex; one hair in the posterior angle; pale fulvous, slightly darker on the lateral margins. Metathorax with sides diverging, posterior angles rounding, with a long hair and short prickle; four hairs on the posterior margin in groups of two in small, uncolored pustulations; posterior margin with a slight angle on the abdomen; pale fulvous, slightly darker on the posterior angle; all of the thorax with a more whitish ground color than the head. Sternal markings consisting of pale intercoxal lines and a very pale median metathoracic blotch. Legs pale fulvous with narrow dark marginal borders.

Abdomen elongate-ovate, tapering rapidly posteriorly; segments with their posterior angles slightly produced, each with from one to three hairs; a transverse series of a few long dorsal hairs near the middle of the segments; ground color pale fulvous, narrow translucent brown bands on the lateral margins; broad transverse pale brown blotches on segments 2 to 7, darker on their inner ends, separated by a broad pale median line, also a broad pale band on the posterior margin of each segment; segment 8 entirely colored, with slight median emarginations on the anterior and posterior margins of the blotch; no distinct lateral bands; last segment round, narrowly emarginate, with one short hair on the posterior margin of each rounding angle; two transverse blotches, one on each side of the emargination.

Giebelia.

Giebelia mirabilis Kellogg.

New Mallophaga, I, 1896, p. 138, pl. xi, figs. 7 and 8.

Many specimens from twenty-seven out of thirty-four individuals shot of the Black-vented Shearwater, *Puffinus opisthomelas*; from ten out of fourteen individuals shot of the Dark-bodied Shearwater, *P. griseus*; from all out of six individuals shot of the Pink-footed Shearwater, *P. creatopus*; from a single individual shot of *P. bulleri*, and from a single individual shot of *P. tenuirostris*, all from the Bay of Monterey, California. Four specimens, probably stragglers from a Short-tailed Albatross, *Diomedea albatrus* (Bay of Monterey, California. The species was described from *P. opisthomelas*.

Oncophorus.

Oncophorus bisetosus Piaget. (Plate VII, fig. 6).

Les Pediculines, 1880, p. 217, pl. xviii, fig. 4.

Several specimens from the Californian Clapper Rail, *Rallus obsoletus* and the Virginia Rail, *Rallus virginianus* (Palo Alto, California). Piaget's specimens were taken from *Rallina plumbeiventris*, *R. tricolor* and *R. isabellina*. He also found specimens on a Yellow Rail, *Porzana noveboracensis* (from North America, in the Museum of Leyden). The specimens from this last bird are distinguished by the varietal name *porzanæ*, being slightly larger than the type specimens and showing certain small differences in hairs and markings. Our specimens from *Rallus obsoletus* and *R. virginianus* agree with var. *porzanæ* in departing in the matter of size and hairs of dorsal surface of abdominal segments from the type specimens, but go farther in differing and must be distinguished by a varietal name.

Var. *californicus* Kellogg and Chapman. (Plate VII, fig. 6). From the Californian Clapper Rail, *Rallus obsoletus* (Palo Alto, California) and the Virginia Rail *Rallus virginianus* (Palo Alto, California). (In the following list of measurements the figures in parentheses are those given by Piaget for the type specimens). Female. Body, length 1.72 mm. (1.35 mm.), width .5 mm. (.47 mm.); head, length .53 mm. (.47 mm.); width .4 mm. (.38 mm); seven hairs on margin of forehead, of which two are longer and dorsal, instead of six with one dorsal as in the types; a prominent hair in the eye not mentioned in the description of the types; two median hairs on dorsal aspect of each abdominal segment, as in the variety *porzanæ* Piaget, instead of four as in the species type. The female has large quadrangular, transverse, lateral abdominal blotches separated by a narrow median uncolored line hardly apparent on segments 6–9; a strong uncolored transverse line between segments 7 and 8; lateral bands black, distinct, segmented. In the male the transverse abdominal blotches are continuous across the segments, with widely separating, uncolored, transverse sutures, especially on posterior half of abdomen.

Oncophorus remotus n. sp. (Plate VII, fig. 7).

A male and female from a Great Gray Owl, *Scotioptex cinerea* (Pullman, Washington). Not at all like *O. heteroceras* Piaget (Les Pediculines, p. 222, pl. xviii, fig. 8) from *Strix bubo*, which has the head varying markedly in the sexes; and not like *O. hexopthalmos* Nitzsch (described by Nitzsch as a *Lipeurus* and referred by Giebel to *Ornithobius*, and by Piaget to *Oncophorus*) from *Strix nyctea*.

Description of the male. Body, length 2.02 mm., width .93 mm.; short, broad; pale golden brown, with slightly darker bands on the head and thorax.

Head, length .65 mm., width .59 mm., subpentagonal, broadly rounding in front; clypeus slightly convex, two hairs on each side of the uncolored clypeal front, a third marginal hair in front of the suture; a long marginal hair and short prickle in front of the trabeculæ which are long and acutely angular; antennæ with its first segment as long as all the other segments taken together, third segment with slight but appreciable distal projection, a few short spines on the segments; eye with a distinct ocular fleck and a long hair; temples with sides nearly straight, two long hairs and two prickles on the margin; occipital margin straight, without hairs or prickles; general color of the head pale golden brown; clypeal signature very pale brown but distinct, anterior margin slightly concave; antennal bands interrupted at the suture, darker chestnut-brown at the posterior extremities, which are turned almost at a right angle with the anterior half and lie half way between the mandibles and base of the antennæ; distinct, angularly contorted, inner bands paler than the antennal bands; occipital bands pale anteriorly, growing darker and more sharply defined near the occipital margin.

Prothorax quadrangular, with rounded posterior angles, with one long hair; sternal markings showing through as dark bands near the lateral margins, bending inwardly before the posterior margin, and separated by a distinct, uncolored median line. Metathorax with convex, divergent sides, a long slender hair and a prickle on the lateral margin, near the posterior angle, three long hairs in the posterior angle; a series of hairs along the rounding, posterior margin. Legs pale brown, with a few scattered spines.

Abdomen broadly elliptical, narrowing at both extremities; a few long hairs in the posterior angles of the segments; a transverse series of hairs on the posterior margins of the segments; segments 5, 6 and 7 narrowed in the middle; last segment narrowly rounding, pointed, with two long hairs on the posterior margin; ground color very pale golden brown; transverse lateral blotches indistinct, separated by a broad uncolored median space, except on segment 5, where the transverse band extends across the entire segment; segments 6, 7 and 8 with a broad median blotch of darker golden brown; segment 9 entirely brown; there are but slight indications of defined lateral marginal bands; genitalia distinct, dark golden brown, broad and complex.

Female. Body, length 2.5 mm., width .93 mm.; head, length .71 mm., width .75 mm. The shape of the head different, the temporal margins being distinctly convex; segments 1 and 2 of the antennæ as long as segments 3, 4 and 5, but segment 2 longer than segment 1. Abdomen widely ellipitical, but distinctly more elongate and less narrowed posteriorly; very pale golden brown; last segment emarginate, with rounding lateral halves.

Eurymetopus.

Eurymetopus taurus Nitzsch. (See Kellogg, New Mallophaga, I, 1896, p. 135, pl. xi, figs. 3, 4, 5 and 6).

Two females from two specimens of the Short-tailed Albatross, *Diomedea albatrus* (Bay of Monterey, California). Previously taken by Kellogg from same host species (same locality). A single immature specimen, probably a straggler, from a Black-vented Shearwater, *Puffinus opisthomelas* (Bay of Monterey, California).

Goniodes.

Goniodes mammillatus Rudow. (See Kellogg, New Mallophaga, II, 1896, p. 509, pl. lxix, fig. 2).

Two immature specimens from a Columbian Sharp-tailed Grouse, *Pediocœtes phasianellus columbianus* (Pullman, Washington). Previously taken by Kellogg from *Callipepla californica* (California).

Colpocephalum.

Colpocephalum perplanum n. sp. (Plate VII, fig. 8).

One specimen from a Tufted Puffin, *Lunda cirrhata* (Bay of Monterey, California). This form resembles

C. latifasciatum Piaget (Supplement, p. 130, pl. xiv, fig. 2), from *Rhynchops flavirostris*. The difference in size, number of hairs of the temples, and character of abdominal segments, together with the unrelated host leads us to make the specimen the type of a new species.

Description of female. Body, length 1.84 mm., width .67 mm.; golden brown, with ill-defined, median, transverse abdominal bands, and small dark brown marginal abdominal blotches; head and thorax with blackish markings.

Head, length .35 mm., width .54 mm.; broadly and flatly rounded in front, with numerous, rather long, and a few short, marginal hairs; one very long marginal hair just in front of the ocular emargination, and two shorter hairs directly on the angle; ocular emargination pronounced and acutely angled interiorly; eye prominent, emarginated, with a large ocular fleck; ocular fringe distinct; antennæ with last segment broad, extending beyond the head; temples with anterior angles rounding, posterior angles angularly meeting the occipital margin; three very long and some shorter hairs on the temporal margin; the occiput slightly concave, with four rather long marginal hairs; a narrow, curving, fuscous band running parallel with the clypeal margin, ending at the lateral extremities in a dark chestnut spot; distinct, black, irregular, ocular blotch; triangular bases of occipital bands blackish brown, connected by an even, occipital border, narrowing medially.

Prothorax broad, lateral angles acute, bearing one long hair and a short spine, sides converging posteriorly, with one long hair in the posterior angles; a series of long hairs on the posterior margin. Mesothorax separated from the metathorax by a distinct, lateral constriction, the posterior margin being distinctly marked with a dark brown band that turns in at the anterior angles along the lateral margins. Metathorax with anterior angles extending beyond the posterior margin of the mesothorax; sides divergent, posterior angles with two long hairs and two short spines; posterior margin straight on the abdomen, with a series of long hairs. Legs robust, concolorous with the metathorax.

Abdomen long, ovate; segments equal, with one or two long hairs and spines in posterior angles, and one or two short spines on lateral margins of each segment; dorsal surface with a single transverse series of hairs along the posterior margin of each segment; the ventral surface with several series of weakly pustulated hairs on each segment; last segment flatly convex, with two dorsal hairs near the lateral margins; ground color pale fuscous, with unevenly colored lateral border of darker fuscous, paling on the outer margins and darkest in posterior angles of segments and along inner margin; a longitudinal, narrow, uncolored, submarginal line parallel with the lateral margin; ill defined, transverse bands slightly darker fuscous.

Colpocephalum funebre Kellogg.

New Mallophaga, I, 1896, p. 147, pl. xii, fig. 7.

One specimen from *Larus heermanni* (Bay of Monterey, California). Described from specimens from *Larus glaucescens* (Bay of Monterey, California).

Colpocephalum pingue Kellogg.

New Mallophaga, I, 1896, p. 144, pl. xii, fig. 5.

One specimen, male, from a Short-tailed Albatross, *Diomedea albatrus* (Bay of Monterey, California). Described from the same host species (same locality).

Colpocephalum spinulosum Piaget. (Plate VII, fig. 9).

Les Pediculines, 1880, p. 563, pl. xlvii, fig. 3.

Many specimens from eight out of fifteen individuals examined of the Sanderling, *Calidris arenaria* (Pacific Grove, California). The specimens agree in all essential details of outline and markings with Piaget's description, showing the characteristic, finely pustulated, dorsal surface of the male, with the single transverse series of long pustulated hairs on each segment in the male and the two series in the female. But there is a marked difference in size, the species type being one-fourth larger than our specimens. Piaget's specimens were taken from *Limosa melanura* (Musuem of Leyden). The American specimens should be distinguished by a varietal name.

Var. *minor* Kellogg and Chapman. (Plate VII, fig. 9). In the following table of measurements the figures in brackets are the dimensions given by Piaget for his type specimens. Male. Body, length 1.72 mm. (2.1 mm.), width .5 mm. (.64 mm); head, length .31 mm. (.38 mm), width .34 mm. (.5 mm). Female. Body, length 2.16 mm. (2.45 mm.), width .7 mm. (.86 mm.); head, length .37 mm. (.38 mm.), width .5 mm. (.5 mm.) From the Sanderling, *Calidris arenaria* (Pacific Grove, California.)

Colpocephalum timidum Kellogg.

New Mallophaga, I, 1896, p. 145, pl. xii, fig. 6.

One specimen from a Black-bellied Plover, *Squatarola squatarola* (Pacific Grove, California). Described from *Charadrius dominicus* (Lawrence, Kansas).

Colpocephalum flavescens Nitzsch. (See Kellogg, New Mallophaga, II, 1896, p. 525, pl. lxxi, fig. 4).

Specimens from the Golden Eagle, *Aquila chrysäetos* (Palo Alto, California) and from a Siberian Eagle, *Haliæetus pelagicus* (brought alive from the Arctic Ocean to California). Taken previously by Kellogg from *Haliæetus leucocephalus* and *Archibuteo lagopus sancti-johannis* (Kansas). Taken by Osborn from "Swallow-tailed Kite" (Ames, Iowa).

Colpocephalum grandiculum n. sp. (Plate VII, fig. 10).

One specimen from a California Towhee, *Pipilo fuscus crissalis* (Palo Alto, California). Also a single specimen, much smaller, (otherwise not indicating immaturity) from a Heerman's Song Sparrow, *Melospiza fasciata heermanni* (Palo Alto, California), which, because of the similarity in outline, characters of legs, and general markings, may be referred to the same species. The species resembles in general shape *C. fumidum* Kellogg (New Mallophaga, II, 1896, p. 523, pl. lxxi, fig. 5) from a California Bush-Tit, *Psaltriparus minimus californicus* (Palo Alto, California).

Description of female. Body, length 2.28 mm., width .81 mm.; head and thorax fulvous, abdomen dull fuscous; small ocular and occipital blotches, very narrow marginal, lateral, abdominal bands; temples produced angularly; a distinct V-shaped uncolored marking between the ocular emarginations, projecting backwards as a more or less distinct uncolored median line through the thorax and abdominal segments 1 to 6.

Head, length .5 mm., width .65 mm.; front broadly rounded, subsemicircular; several hairs on the strictly anterior margin, two rather long hairs on the lateral margin of the front, and two long hairs in front of the ocular emargination; eye distinct, almost if not quite divided, the larger and anterior portion lying in the angle of the ocular emargination, while the smaller, posterior portion lies apparently on a ridge that extends back across the temples; temples prominent; anterior margin almost at right angles with the median line of the head; ocular fringe prominent, extending as far as the anterior temporal angle, a few short hairs on this angle, two long hairs and a few short spines on the lateral margins and the posterior rounding angles; occipital margin medially convex; head smoky, fulvous, distinct, with slightly darker bands extending towards the lateral margin from the base of the mandibles which are dark brown; a V-shaped uncolored marking, each branch extending from the slight swelling in front of the ocular emargination back two-thirds of the distance to the occipital margin, where the uncolored lines meet at the apex of the V; ocular blotches black, even, angular, extending forward as far as the uncolored branch of the V; temples very narrowly bordered with dark brown on the posterior angles; occipital blotches dark brown to black, sharply defined except on the anterior extremity, where they send out a sharp angular blotch; lateral extremities long and gradually narrowing, inner extremities blunt, separated by a fulvous median space.

Prothorax, lateral angles bluntly rounding, with one long hair and a short spine; lateral margin slightly concave, latero-posterior angles with no hair; posterior margin rounding on the mesothorax; two long hairs on the posterior margin near the lateral posterior angles; evenly fulvous, slightly darker on the lateral margins; chitin transverse and longitudinal bars distinct. Mesothorax with sides diverging, posterior angles slightly protruding, separated distinctly from the metathorax, a long hair on the lateral margin, a dark marginal band on the anterior angles. Metathorax narrow, sides diverging, posterior angles rounding, posterior margin straight, with one long hair, one short hair, and a short spine; narrow dark brown marginal band on the anterior angle and lateral border; faint indications of an uncolored longitudinal median line. Legs robust; femora broad; fulvous with darker markings on the border; a series of short hairs on the outer margin of the tibia. Sternal markings consisting of intercoxal lines, a distinct shield-shaped median blotch on the prothorax, a narrow median darker longitudinal blotch between the pro- and mesothorax, a larger median blotch between the second and third pair of legs, with a distinct triangular anterior portion and a quadrangular posterior portion.

Abdomen broadly elongate; posterior angles projecting but little, with one long hair in each angle, and a series of dorsal hairs on the posterior margin of each segment; segments widely separated by uncolored sutures; transverse lateral blotches fuscous, darkening on the lateral margins into narrow bands; segments 1 to 5 with the transverse blotches separated by a narrow uncolored median line; segments 5 to 8 entirely dark fuscous; last segment with broadly rounding posterior margin, one long and one short hair each side and a series of short hairs on the posterior margin; color an even fuscous. Ventral surface a small median triangular fuscous blotch on segment 1; transverse blotches uninterrupted, but the posterior margin of the blotches on segments 2 to 6 emarginated, darker fuscous on the posterior margin; a double series of pustulated hairs and a few scattered hairs on each segment.

Ancistrona.

Ancistrona gigas Piaget. (See Kellogg, New Mallophaga, I, 1896, p. 150, pl. xiii, figs. 1 and 2).

A few specimens from the Shearwaters, *Puffinus opisthomelas* and *P. griseus* (from one individual of *opisthomelas* out of thirty-four examined, and from two of *griseus* out of fourteen examined) from the Bay of Monterey, California. Taken previously by Kellogg from *Fulmarus glacialis* vars. *rodgersii* and *glupischa* (Bay of Monterey, California).

Trinoton.

Trinoton luridum Nitzsch. (See Kellogg, New Mallophaga, I, 1896, p. 152, pl. xiii, fig. 4).

Specimens from the Baldpate, *Anas americana,* and the American Scaup Duck, *Aythya marila nearctica,* (Palo Alto, California) and from the Shoveller, *Spatula clypeata* (Mountain View, California). Taken previously by Kellogg from two of these hosts, and from other duck species (Kansas and California).

Trinoton lituratum Nitzsch. (See Kellogg, New Mallophaga, I, 1896, p. 151, pl. xiii, fig. 3).

Specimens from the Shoveller, *Spatula clypeata* (Mountain View, California) and from another individual of the same species (Palo Alto, California). Taken previously by Kellogg from *Dafila acuta* and *Merganser americanus* (Lawrence, Kansas).

Menopon.

Menopon tridens Nitzsch. (See Kellogg, New Mallophaga, I, 1896, p. 165, pl. xv, figs. 3 and 4).

Specimens from an American Eared Grebe, *Colymbus nigricollis californicus* (Bay of Monterey, California); from the Western Grebe, *Æchmophorus occidentalis* (one bird from Washington, and one from California); and from the Californian Clapper Rail, *Rallus obsoletus* (three birds), and the Virginia Rail, *Rallus virginianus* (Palo Alto, California). Taken previously by Kellogg from the two hosts first named, and from *Urinator lumme* (California).

Menopon infrequens Kellogg.

New Mallophaga, I, 1896, p. 161, pl. xv, fig. 5.

Ten specimens from *Larus delewarensis* (Bay of Monterey, California). Described from a single female from *Larus glaucescens* (Bay of Monterey, California). The male is much smaller than the female, as shown by following measurements: body, length 1.4 mm., width .6 mm.; head, length .25 mm., width .53 mm.

Menopon irrumpens n. sp. (Plate VIII, fig. 1).

Four specimens from a Short-tailed Albatross, *Diomedea albatrus* (Bay of Monterey, California). No *Menopon* has been hitherto taken from an Albatross.

Description of female. Body, length 2.23 mm.; width 1.01 mm.; short, broad; dark chestnut-brown with darker blotches on the head and lateral bands on thorax and abdomen.

Head, length .4 mm., width .74 mm.; wide through the temples; clypeus broad, with a slightly angulated front; one rather long and one shorter marginal hair each side of the angular point of the clypeus, a short prickle near the suture; three long marginal hairs on the slight swelling in front of the ocular emargination, two short hairs in front of these, nearer the suture;

ocular fringe distinct, composed of stiff curving hairs which extend slightly on the temporal margin; temples with posterior angles produced; four long pustulated hairs, two shorter hairs, and one short spine on the margin; occipital margin concave, with a series of six long pustulated hairs and one spine; color of the head light chestnut-brown, with dark brown ocular blotches and black ocular fleck, and dark chestnut markings in front, near the mandibles, which show through the head distinctly; occipital margin with a narrow chestnut band, darkening into broad occipital blotches.

Prothorax broad, sides rapidly converging posteriorly; lateral angles narrowly rounding, with a short spine and a long pustulated hair in the angle, a series of fourteen strong hairs along the convex posterior margin; general color dark chestnut-brown, except the space above the conspicuous dark transverse chitin bar, which is pale fuscous; the longitudinal bars, at the ends of the transverse bar, are narrow but distinct. Metathorax short, hardly broader than the prothorax; sides divergent, with two spines on the lateral margins; two long hairs and two short spines on the posterior angles; a series of long pustulated hairs on the posterior margin not so heavy, however, as those of the prothorax; color chiefly dark chestnut-brown, transverse band darkening into a narrow black line along the lateral margin, and into a broad triangle in the posterior angles; in front of this dark band, a pale, broad, mesosutural band, and in front of this the pale brown mesothorax. Legs of the palest fuscous of the prothorax, with several short, stiff hairs on the femora and tibia.

Abdomen broadly elliptical, with several short spines on the lateral margins of the segments, and from one to five long hairs in the posterior angles; a series of long hairs on the posterior margin of each segment; transverse blotches of dark chestnut-brown continuous across the segments, with but a very narrow, pale, posterior marginal line; the lateral marginal bands are wide and distinctly darker brown, and they do not reach the posterior margins; the last segment broadly emarginate, with two long, dorsal hairs on the rounded, posterior angles, and two very short spines on the inner margin of the emargination; the ventral surface with dark transverse bands and a series of hairs along the posterior margin of each segment.

Menopon paululum n. sp. (Plate VIII, fig. 2).

Specimens from three out of thirty-four individuals shot of the Black-bodied Shearwater, *Puffinus opisthomelas*, from two out of fourteen shot of *Puffinus griseus*, and from two specimens out of six shot of *Puffinus creatopus*. The first *Menopon* species recorded from *Puffinus*. The new species shows no special resemblance to forms taken from allied birds, like Fulmars.

Description of the male. Body, length 1.13 mm., width .5 mm.; small, pale yellow with distinct brown ocular blotches; abdomen with golden transverse bands and brown marginal blotches.

Head, length .26 mm., width .38 mm.; front rounding, with four short hairs on the margin, one marginal hair at the suture, three long and one short hair in front of the ocular emargination which is distinct but shallow, with an ocular fringe; maxillary palpi long, last two segments extending beyond the margin of the head; eyes inconspicuous but with a distinct ocular fleck; temples but little expanded, with four long hairs and several short spines on the angles; occipital margin but slightly concave; head pale yellow with a brown spot just outside the mandibles connected with them by a narrow brown band; mandibles dark, showing through the head; ocular blotches small, narrowing posteriorly; occipital margin with a narrow brown band and small occipital blotches.

Prothorax with anterior angles slightly produced, a short prickle and a long hair in the angle, a series of long hairs on the rounding posterior margin; transverse and longitudinal chitin bars pale yet distinct; no blotches. Metathorax with slight lateral emargination; posterior margin nearly straight, with a series of spiny hairs; a pale golden, narrow, mesothoracic, transverse band, and similarly colored, wider, metathoracic bands. Legs pale golden; femora thick. A median prosternal blotch, shield-shaped, with a lateral process projecting backward and outward; metasternum with a pale median blotch from which short spiny hairs arise.

Abdomen elliptical, with posterior angles of the segments slightly produced, a few short spines on the lateral margins, and one or two long hairs and short spines in the posterior angles; a series of stiff hairs along the posterior margin of the segments, those on the last segments being longer; on the ventral surface two transverse series of short spiny hairs on each segment; pale golden transverse bands extending across the segments to shiny brown subcircular marginal blotches; last segment rounding behind, without marginal blotches, and with a few longish hairs.

Female. Body, length 1.74 mm., width .67 mm.; head, length .27 mm., width .45 mm., thus being much longer than the male; transverse bands of the abdomen rather more distinct than in the male, the uncolored sutural bands being thus made also more distinct, each segment with posterior series of hairs; last segment with six stiff hairs on each rounding angular portion of the posterior margin, and the median straight portion with an uncolored border and fringe of fine hairs.

Menopon petulans n. sp. (Plate VIII, fig. 3).

One specimen from a Black-bodied Shearwater, *Puffinus griseus* (Bay of Monterey, California). Shorter, broader, and darker colored than *paululum* n. sp. from *Puffinus opisthomelas* (same locality).

Description of male. Body, length 1.34 mm., width .68 mm.; short, broadly elliptical; head with distinct ocular emargination and projecting temples; general color dark fuscous with distinct, large black ocular blotches; transverse abdominal bands fading in their medial portions but distinct laterally.

Head, length .28 mm., width .53 mm.; front rounded, with a very slight median angulation; a rather long median hair each side of the front angulation; a short marginal prickle in front of the suture, one rather long marginal hair just back of the suture; two pustulated hairs and one long spine in front of a distinct ocular emargination; eye distinct, filling base of ocular emargination with a black ocular fleck; temples rounding, projecting, with three long hairs and several spines; occipital margin concave, with six long hairs and two spines on the margin; front of the head with slightly darker brown triangular blotches each side of the pale front; mandibles showing through the head as a dark brown spot; ocular blotch broad and distinctly black, fading gradually along the temporal margin; occipital bands faintly showing; occipital blotches distinct, being connected by a narrow black band which fades on the temporal margins.

Prothorax with lateral angles narrowly rounding, with one long hair and a short spine, a series of long hairs on the rounding posterior margin; lateral blotches but little darker on the margins; transverse chitin bar distinct, but little darker than the fuscous ground color of the prothorax. Metathorax short, lateral margins slightly divergent, a little concave, a short prickle near the posterior angles and a long hair and one short spine in the angle; a series of hairs along the weakly convex posterior margin; lateral blotches distinct, meeting on the median line; darker brown to black on the lateral margins, a pale band on the posterior margin. Legs robust, pale fuscous with darker marginal markings. Sternal markings consisting of a distinct median blotch, with rounded anterior margins, posterior angles projecting backward, posterior margin also produced into a distinct angle.

Abdomen broadly elliptical, segments with short spines on the lateral margins and a few long hairs in the posterior angles; a series of dorsal, spiny hairs on the posterior margin of each segment; general color of the abdomen dark fuscous; lateral blotches distinct, black on the lateral margins, paler and fading out medially on the segments before segment 7; segments 7 and 8 with continuous transverse bands; segment 9 wide, with two lateral blotches meeting narrowly on the median line and a paler band on the lateral margin; the last segment flatly rounding; two short hairs on the posterior margin; ventral markings very similar to those of the dorsal surface, also a similar series of hairs on the posterior margins of the segments.

Menopon titan Piaget. (See Kellogg, New Mallophaga, I, 1896, p. 163, pl. xv, fig. 2).

One male from a Brandt's Cormorant, *Phalacrocorax penicillatus* (Bay of Monterey, California). This specimen differs from every other individual of this curious species that I have yet examined. It is smaller than var. *linearis*, the blotches of thorax are different, and the incomplete series of pustulated hairs along the posterior margins of the abdominal cross-bands conspicuously differ from the usual condition in *titan*. *Titan* has not before been taken from any other bird than a pelican, and this single individual from a cormorant may be a straggler. If so, it must have come from *Pelecanus californicus*, the only species of pelican found in the Bay of Monterey.

Var. *incompositum* Kellogg and Chapman. (Plate VIII, figs. 4 and 5). Male, body, length 4.6 mm., width 1.66 mm.; head, length .62 mm., width 1. mm.; the smallest variety of *titan* yet noted; mesothorax with a narrow transverse blackish band continuous across the segment; metathorax with triangular, blackish, lateral blotches, apex projecting inward; abdominal segments 1–8 with continuous, blackish, transversal bands, paler on segments 7 and 8; an incomplete series of pustules (six complete and prominent on segments 3–6) along posterior margin of each transverse band; last segment with a small transversal linear blotch on each side; genital blotch on underside of segment 8 composed of two lateral triangles partly overlapping a central shield, from which projects anteriorly a sharp, distinct, linear process; laterad of this central compound blotch there is on each side a weakly curving, blackish, diagonal, linear blotch. Found on Brandt's Cormorant, *Phalacrocorax penicillatus* (Bay of Monterey, California).

Menopon titan var. **linearis** Kellogg.

New Mallophaga, I, 1896, p. 163, pl. xv, fig. 2.

Many specimens from the Californian Brown Pelican, *Pelecanus californicus* (Bay of Monterey, California). Described from the same host species, same locality.

Menopon funereum n. sp. (Plate VIII, fig. 6).

A single male from a Gairdner's Woodpecker, *Dryobates pubescens gairdnerii* (Sunol, California), and a pale male from a Western Evening Grosbeak, *Coccothraustes vespertinus montanus* (California). This second specimen determined with doubt. Not like *M. pici* Denny (Monograph. Anoplur. Brit., p. 219, pl. xx, fig. 5; Piaget, Supplement, p. 93, pl. x, fig. 3) from *Picus viridis;* also differing distinctly from *M. præcursor* Kellogg (Mallophaga from Birds of Panama, Baja California, and Alaska, in New Mallophaga, III, 1899, p. 46, pl. iv, fig. 8) from *Melanerpes uropygialis* (Baja California).

Description of the male. Body, length 1.5 mm., width .59 mm.; mostly dark colored because of the strong, continuous, brown, transverse, abdominal bands and the blackish marking of the head, thorax and legs; thorax long, with mesothoracic sutural line distinct under magnification.

Head, length .4 mm., width .56 mm.; front convex, with two marginal hairs near the median line of the front, a short prickle midway between this hair and a long hair and short spine which are on the angle in front of a slight lateral concavity, in which are a long hair and short prickle; a long hair and shorter hair near the posterior angle of the concavity and in front of the angle before the ocular emargination on which are two long hairs; eye large, filling the inner angle of the ocular emargination, distinctly emarginate and with a large black ocular fleck; a rather long hair on its dorsal surface near the margin; a distinct ocular fringe; temple meeting the ocular emargination angularly; fine, long, pustulated hairs and some short spines on the temporal margin; occipital margin concave, with two long hairs near the median line; ground color of the head pale fuscous with dark blackish brown blotches each side of the front; ocular blotches broad, distinct on the posterior margin but fading anteriorly till they color the angle in front of the ocular emargination; temples narrowly and irregularly bordered with dark brown; occipital margin with a defined blackish brown band, widening into angular occipital blotches; distinct occipital signature.

Prothorax short; anterior angles inconspicuous, with two spines; posterior margin with a series of long hairs; ground color dark fuscous, with distinct chitin bars. Mesothorax and metathorax long, being separated by a narrow, uncolored suture and slight lateral emargination, mesothorax dark on the anterior portion; metathorax with distinct dark chitin bars. Sternal markings consisting of dark intercoxal lines; prothorax with distinct median blotch of pale fuscous, a distinct V-shaped chitin bar longitudinally across it; dark median blotches on the meso- and metathorax. Legs large, pale fuscous with dark marginal borders and semiannulations; scattered hairs and spines.

Abdomen short, broadly elliptical, small as compared with the large head and thorax, which are together longer than the abdomen; a series of long hairs on the posterior margin of each segment and a few short spines and hairs in the posterior angles; each segment with a broad, dark, transverse band, darker on the lateral margin and covering almost all of the segment; a longitudinal, submarginal, pale band, parallel with the lateral margins of the abdomen; last segment broadly rounded, with several long hairs near the lateral margin and some shorter hairs on the posterior portion of the segment; ventral surface with at least one series of short pustulated hairs on the posterior margin of each segment; genitalia distinct, angular, extending far forward in the body.

Menopon distinctum n. sp. (Plate VIII, fig. 7).

Specimens from two specimens of the Ash-throated Flycatcher, *Myiarchus cinerascens* (Palo Alto and Ontario, California), and from a Cactus Wren, *Heleodytes brunneicapillus* (Ontario, California). A well marked form.

Description of the female. Body, length 1.5 mm. width .62 mm., elongate-ellipitical; pale translucent fuscous with blackish brown ocular blotches; black ocular fleck and small blackish spots on the lateral margins of the front; dark transverse blotches on the abdomen; a distinct pale submarginal longitudinal line parallel with the lateral margin of the abdomen.

Head, length .31 mm., width .46 mm.; parabolic, wide through the temples; front broadly rounding, a slight angulation in front; one hair each side of this angulation; two hairs on the lateral margin of the front; two long hairs on a slight swelling in front of a distinct ocular emargination; one long and two short hairs on the dorsal surface, in front of the ocular emargination; eye large, filling the angle of the emargination and extending on the temple, with a slight constriction; a short spine on the posterior portion, and a large black ocular fleck; ocular fringe made up of comparatively few stiff spines, more numerous on the outer margin in front of the temples; two long hairs and several shorter hairs on the temporal margin; occipital margin nearly straight, with two long and two short hairs; pale translucent fuscous; mandibles dark, showing through the front; a dark spot on the lateral margin of the front outside the base of the mandibles; ocular blotches dark brown to black, extending forward as far as the dark lateral blotches, but paler chestnut-brown anteriorly; dark narrow border on the occiput, occipital bands pale yet distinct.

Prothorax with convex lateral margins; a short spine in the anterior angle; a few spines on the lateral margin; a series of long hairs on the rounding posterior margin; fulvous, with dark transverse and longitudinal chitin bars distinct. Mesothorax wide, with strongly divergent sides; a few spines on the lateral margin; one long hair and several spines in the posterior angle; dark inner chitin bars extending along the anterior angle and back across the segment; a second chitin bar extending from the lateral margin back across the metathorax; the posterior angle of the mesothorax dark fuscous, otherwise the segment is pale translucent fuscous. Metathorax narrow; a long hair and a short spine in the posterior angles; dark lateral triangular blotches, fading inwardly. Legs long, pale translucent fuscous, with dark fuscous borders and semiannulations; many short spines on the femora. Sternal markings consisting of distinct brown intercoxal lines and a pale but distinct wedge-shaped median blotch.

Abdomen broadly elliptical; several spines on the lateral margins of the segments; some long hairs in the posterior angles; many dorsal spines, not arranged in any definite series on the segments; lateral marginal blotches dark fuscous, separated from the median transverse blotches by a pale submarginal band, parallel with the lateral margin of the abdomen; median transverse blotches paler fuscous; transverse bands of segments 1 to 6 widely separated by uncolored sutural bands; last segment rounding, with a fringe of hairs on the posterior margin, dark transverse blotch narrowed distinctly in the middle, ventral transverse bands distinctly fuscous; many hairs arranged nearly in two definite series in each segment.

Male. Body, length 1. mm., width .59 mm.; head, length .25 mm., width .5 mm.

Menopon persignatum n. sp. (Plate IX, fig. 1).

Many specimens from the California Jay, *Aphelocoma californica* (2 specimens, Mountain View, California). Resembling in general shape and characters the three or four species of *Menopon* described by Nitzsch and Piaget from the European Jays.

Description of the female. Body, length 2.03 mm., width .75 mm.; long, narrow; pale fuscous with distinct black ocular blotches, blackish lines in the thorax, and broad dark fuscous transverse abdominal bands.

Head, length .34 mm., width .56 mm,; front broadly but slightly angularly rounding; no hairs on the frontal margin, one long and two shorter hairs on the lateral margins of forehead, besides two long hairs just in front of the ocular emargination, which is nearly filled by the large eye which is slightly emarginated and bears a short prickle; ocular fringe with only a few hairs of uneven length; temples produced, rather narrowly rounded, with five long hairs and several short hairs and spines on the margin; occipital margin straight in its middle portion; one long and one short hair near the posterior margin, and one hair on each side of the median line; ground color of the head fuscous with distinct, curving, linear blackish ocular blotches; an indistinct brown occipital signature with anterior angles produced laterally.

Prothorax large, lateral angles with one long hair and a short spine, two long hairs in the broadly rounded posterior angle and a series of six long hairs on the straight posterior margin. Mesothorax with four or five short spines on the lateral margin and two long hairs and two spines in the posterior angle; a series of stiff hairs along the posterior margin. Metathorax with a series of stiff hairs on its posterior margin, and in the posterior angle one long hair and two spines; ground color of the thorax is pale fuscous, no distinct blotches, but dark transverse and longitudinal chitin bars on the prothorax; curving chitin bars on the anterior angle of the mesothorax, and a pair of chitin bars extending from the anterior half of the lateral margin of the mesothorax back across the metathorax as far as the third pair of coxæ. Sternal markings consisting of dark intercoxal lines; on the prothorax a small median blotch with the posterior angles extended in dark chitin bars which extend forward to the anterior margin; the posterior margin of the blotch extends back in a narrow point; a large wedge-shaped blotch between the second and third pair of coxæ; this blotch has a series of short pustulated hairs on its anterior and lateral margins. Legs pale fuscous with narrow dark borders.

Abdomen elongate-elliptical; two long hairs and short spines in the posterior angles; a series of short hairs on the posterior margin of each segment, growing more stiff and spine-like near the lateral margin; broad dark fuscous transverse bands separated by broad pale sutural bands; darkening laterally to form broad dark lateral bands, set off by rather broad pale submarginal, longitudinal bands; last segment flatly rounding, with a fringe of fine hairs; ventral surface with similar markings, but with an irregular median transverse series of hairs, besides the series on the posterior margin of the segment.

Male. Body, length 1.43 mm., width .75 mm.; head, length .28 mm., width .56 mm., thus being much smaller than the female; also of short, broad, oval shape rather than elongate and narrow; darker and more evenly fuscous; pale submarginal longitudinal bands parallel with the sides of the abdomen less distinct than in female; transverse bands narrow and less definite; lateral blotches narrow and darker on the posterior margin of the segments; last segment slightly angular, with a fringe of hairs; genitalia faintly distinguishable through the body, extending forward into segment 7.

Menopon incertum Kellogg.

New Mallophaga, II, 1896, p. 533, pl. lxxiii, fig. 2.

Many specimens from a Russet-backed Thrush, *Turdus ustulatus* (Palo Alto, California); a Western Lark Sparrow, *Chondestes grammacus strigatus* (Ontario, California); and a Vigor's Wren, *Thryothorus bewickii spilurus* (Palo Alto, California). Taken previously by Kellogg from *Turdus ustulatus* and from the American Goldfinch, *Spinus tristis* (same locality).

Menopon mæstum n. sp. (Plate IX, fig. 2).

Two specimens from a Golden-crowned Sparrow, *Zonotrichia coronata* (Palo Alto, California), and a

Samuel's Song Sparrow, *Melospiza fasciata samuelis* (Palo Alto, California). A short, broad species, with short, wide head, and wide prothorax, approaching the *Eureum* type of Menopon (see p. 133 this paper).

Description. Body, length 1.37 mm.; width .81 mm.; short, broad; head very short and wide, not of the usual evenly crescentic type; occipital margin straight and dark; general color dark fuscous, the dark markings of the head making the posterior portion appear quadrangular.

Head, length .28 mm., width .59 mm.; front broad, flatly rounded; six hairs on the front, one each side of the angulation and three (one long and two shorter) hairs on the lateral margins of the front; two hairs on the angle in front of the ocular emargination; lateral margin of the forehead almost at right angles with the lateral margins of the front; eye large, prominent, with a large black ocular fleck and a short spine; ocular fringe sparsely spined; temples projecting strongly, and narrowly convex, with three long hairs and several shorter hairs and spines; occipital margin straight; a narrow broad submarginal band across the front, its posterior ends bending in so as to leave clear pale brown the anterior portion of the angle in front of the ocular emargination; from this angle a distinct dark fuscous quadrangular blotch extends back to the occipital margin, cutting off the rounding temples which are very pale fuscous; ocular blotches narrow and dark, extending forward along the ocular emargination, meeting the anterior margin of the dark fuscous blotch interrupting the arms of the narrow uncolored V-shaped marking, which has its branches rising from the inner angle of the ocular emargination and its vertex on the occipital margin; occipital blotches blackish brown, connected by a narrow even line on the occipital margin; a dark broad occipital signature showing through the head.

Prothorax short and wide; two short spines in the anterior margin and a series of four long pustulated hairs and one short spine on each rounding lateral and posterior margin; transverse and longitudinal chitin bars distinct; median portion of the prothorax pale anteriorly, but darker fuscous towards the posterior margin; lateral portions, beyond the longitudinal chitin bars, dark fuscous. Mesothorax narrow; posterior angles distinctly angular, with a long hair and spine; dark transverse band on the posterior margin, dark longitudinal chitin bars extending from the anterior angles across the mesothorax; a second pair of chitin bars extending from the anterior, lateral margins back across the metathorax. Metathorax narrow, appearing like the first abdominal segment; a long hair and two spines in the posterior angle; a dark brown transverse band across the lateral margin. Sternal markings consisting of dark intercoxal lines, a median blotch on the prothorax, with the posterior angles produced laterally, meeting narrow dark chitin bars which extend forward to the anterior margin; the posterior margin of the blotch also produced in an angle; a broad brown median band between the second and third pair of legs, also extending onto the first abdominal segments; a few scattered pustulated hairs on this band. Legs large, pale fuscous, with narrow dark borders and scattered hairs.

Abdomen broadly ovate, the poles broadly truncate; posterior angles projecting, with one or two long hairs and a short spine; segments narrower on the anterior half of the abdomen; a few hairs on the posterior margin of the segments; entire abdomen a dark rich fuscous, darker on the posterior margins of the segments; last segment broad, narrow, with a fringe of hairs along the rounding posterior margin.

Menopon malleus Nitzsch (Plate IX, fig. 3).

Germar's Mag. Ent., 1818, vol. iii, p. 301.

Eureum malleus Nitzsch, Burmeister, Handb. d. Ent., 1840, vol. ii, p. 441; Denny, Monograph. Anoplur. Brit., 1842, p. 288; Giebel, Insecta Epizoa, 1874, p. 249; Piaget, Les Pediculines, 1880, p. 608, Supplement, 1885, p. 139, pl. xv, fig. 3.

A single immature specimen from a Cliff Swallow, *Petrochelidon lunifrons* (Ontario, California), and an adult female and an immature specimen from a Cactus Wren, *Heleodytes brunneicapillus* (Ontario, California). The single specimen of this species previously known was collected by Nitzsch in 1814 from *Hirundo rustica*. As the above named Cliff Swallow and Cactus Wren were collected by the same person on the same day *it may be* that the two individuals taken from the wren are stragglers from the swallow.

This species has heretofore been attributed to the genus *Eureum* Nitzsch, the genus being based upon the single specimen (which, though heretofore apparently not so considered, is immature) of this species and a very few specimens of another very different species, *cimicoides* Nitzsch from the European Swift *Cypselus apus*. Piaget has suspected that both these species are merely rather aberrant members of the genus *Menopon*, which position, as regards the species *malleus*, at least, we take unqualifiedly. The two species have been held together partly through the usual conception of the near relationship of the hosts; as Nitzsch says, "*habitatio in chelidonum familia*" (Germar's Mag. Ent., vol. iii, p. 301, 1818). Now, in fact, the swallows and the swifts are not nearly related at all, the swifts finding their near relations among the night-hawks and hummingbirds. The finding of an immature and an adult female together on the wren, in addition to a single immature specimen on the swallow, allows us to present new evidence of the agreement of the species in generic characters with *Menopon*. The *Menopon* species, *mœstum*, described in this paper, serves as an easy step from the more typical *Menopon* type to this peculiar *Eureum* type with its short, broad head, its short, broad prothorax, and long, heavy legs. *Menopon robustum* Kellogg (New Mallophaga, II, 1896, p. 528, pl. lxxii, fig. 3) is of this gradatory type, and presents "a mingling of characters of *Menopon*, *Ancistrona*, and *Eureum;* a short, broad head with strongly chitinized, backward-projecting processes on the ventral surface like *Ancistrona;* a thorax like *Eureum;* and the habitus and general body characters of *Menopon*" (Kellogg, l. c.). Osborn's *M. expansum* (Insects Affecting Domestic Animals, U. S. Dept. Ag., Div. Ent., Bull. N. S., No. 5, 1896, p. 245, pl. ii, fig. *j*.) from *Dolichonyx oryzivorus* must also be of this general type.

Our immature forms correspond with the description and figure (Piaget, Supplement, p. 139, pl. xv, fig. 3) of the species. Our adult female (figured herewith) shows the following characters not referred to, or unconformable to those in Piaget's description. Body, length 2.25 mm., width 1.15 mm.; head, length .34 mm., width .9 mm.; head less flatly rounded in front than in the young, and with a slight median angulation; on each side of this angulation a conspicuous marginal hair, and farther to the side a longer hair not marginal, but rising from just in front of the base of the antenna. Metathorax with two long hairs and three spines in the posterior angles, the three spines ranged along the posterior margin. Dorsal surface of the abdomen with a few scattered, longish hairs; ventral surface with groups of short, strong spines and some longish hairs on the lateral part of the posterior margins of segments; last segment broadly rounded behind, with fringe of weak hairs of different lengths.

Menopon ridulosum n. sp. (Plate IX, fig. 4).

Specimens from two Yellow Warblers, *Dendroica æstiva* (Palo Alto, California). A small, heavy-bodied form.

Description. Body, length 1. mm., width .53 mm.; being thus a very small species; head large compared with the rest of the body; head almost as wide as long; abdomen with narrow transverse abdominal bands.

Head, length .46 mm., width .51 mm.; large, nearly as broad as the abdomen; front broadly parabolic, with a slight median angulation; two short hairs in front each side of the angle, several shorter hairs in the frontal margin, two longer hairs on the lateral margin, and two long hairs on the angle before the shallow ocular emargination; eye with a black ocular fleck; ocular fringe distinct; two very long hairs on the narrowly rounding temples and several short spines; occipital margin concave, with four long hairs on the margin; two small angular blackish spots on the lateral margin of the front outside the mandibles, which are also dark, showing through the head; ocular blotches curving, blackish brown, fading on the anterior portion of the ocular emargination; a narrow band of dark blackish brown on the occipital margin.

Prothorax wide; a long hair and short spine on the anterior angle; a series of long hairs on the rounding posterior margin; dark transverse and longitudinal chitin bars distinct, dark brown, while the ground color of the prothorax is even pale fulvous. Mesothorax long, with strongly diverging sides; posterior angles sharp, with several long hairs and broad heavy spines; a series of hairs on the posterior margin; ground color pale fulvous with distinct, narrow chitin bars extending from the anterior angles across the mesothorax, a second pair of chitin bars extending from the lateral margins across the meso- and metathorax. Metathorax narrow; posterior angles with a few long hairs and heavy spines; posterior margin with a series of hairs; intercoxal lines showing through the thorax. Legs pale fulvous with darker marginal markings.

Abdomen broadly elliptical, short; posterior angles with one or two long hairs and some heavy spines; a series of hairs on the posterior margin of the segments, which give place to heavy spines near the lateral margin; a few scattered dorsal spines; last segment flatly rounded, with a few short marginal spines; narrow dark fuscous transverse bands, separated by broad pale transverse bands.

Physostomum.

We have representatives of this genus from a dozen species of passerine birds, but we do not feel able to make satisfactory specific determination of our material except in a few instances. We do not believe that under the present knowledge of the group much can be done toward distinguishing any but peculiar and obviously characterized species, forms readily separable by marked peculiarity of shape. We have specimens of this genus from the following birds, all from California: Western Wood Pewee, *Contopus richardsonii* (two specimens); Say's Phœbe, *Sayornis saya*; Western

Flycatcher, *Empidonax difficilis*; Ash-throated Flycatcher, *Myiarchus cinerascens*; Spurred Towhee, *Pipilo maculatus megalonyx*; California Towhee, *Pipilo fuscus crissalis*; Cedar Waxwing, *Ampelis cedrorum*; Samuel's Song Sparrow, *Melospiza fasciata samuelis*; Least Vireo, *Vireo bellii pusillus*. In addition, we distinguish the three following species of the genus.

Physostomum sucinaceum Kellogg.

New Mallophaga, II, 1896, p. 514, pl. lxx, fig. 2.

Three specimens from a Western Flycatcher, *Empidonax difficilis* (Palo Alto, California). Previously taken by Kellogg from the same host (same locality).

Physostomum diffusum Kellogg.

New Mallophaga, II, 1896, p. 518, pl. lxx, fig. 3.

One specimen, var. *pallidum* Kellogg from an Oregon Junco, *Junco hyemalis oregonus* (Pullman, Washington). Taken previously by Kellogg from *Junco* sp. (Lawrence, Kansas).

Physostomum prominens n. sp. (Plate IX, fig. 5).

Two specimens from a Costa's Hummingbird, *Calypte costæ* (Ontario, California). This strange form with its lateral head margins deeply sinuate and its unique prothorax is very different from any other *Physostomum* described. The specimens are probably not fully mature, one distinctly immature, the other lacking probably only coloration intensity.

Description. Body, length 2 mm., width .85 mm.; transparent whitish; head short and broad, with deeply sinuous lateral margins; eyes in the posterior angles.

Head, length .5 mm., width .53 mm.; broad, short; front broad, straight; conspicuous projecting lateral palettes; the lateral margins of the head deeply concave before the middle; temples swollen, the margins convex; head widest across the posterior angles which are not produced backwards, but rounding rectangular; the inconspicuous eyes with conspicuous black flecks are situated in the very apex of these angles; each angle bears two longish hairs and one shorter one; posterior margin nearly straight, feebly angulated in the middle; whole head transparent whitish with faint brownish tinge here and there.

Prothorax large, lateral margins with lateral angles broadly and bluntly rounded; posterior margin almost semicircular, with four rather short hairs on each lateral half; pale transparent whitish with faint brownish at margins. Metathorax with rapidly diverging lateral margins, straight posterior margin with two hairs and a spine in region of posterior angles, three hairs near posterior margin just inside of this region, and two hairs and a spine anterior to these submarginal hairs.

Abdomen broadly elliptical; posterior angles not projecting and without conspicuous hairs; on the lateral portion of each segment a group of three hairs near the posterior margin, and a hair and a spine near the lateral margin and more anterior; pale transparent whitish with a pale brown narrow submarginal longitudinal band fading posteriorly.

LIST OF HOSTS WITH PARASITES.

- Æchmophorus occidentalis.
  - Menopon tridens.
- Colymbus nigricollis californicus.
  - Nirmus fusco-marginatus var. americanus.
  - Menopon tridens.
- Lunda cirrhata.
  - Nirmus pacificus.
  - Colpocephalum perplanum.
- Cerorhinca monocerata.
  - Nirmus maritimus.
- Ptychoramphus aleuticus.
  - Nirmus maritimus.
- Synthliboramphus antiquus.
  - Nirmus maritimus.
- Cepphus columba.
  - Docophorus procax.
  - Nirmus pacificus.
    - fusco-marginatus var. americanus.
- Stercorarius pomarinus.
  - Docophorus melanocephalus.
  - Nirmus triangulatus.
  - Lipeurus laculatus.
- Rissa tridactyla pollicaris.
  - Nirmus lineolatus var. atrimarginatus.
- Larus occidentalis.
  - Docophorus lari.
- Larus argentatus smithsonianus.
  - Nirmus fusco-marginatus var. americanus.
- Larus vegæ.
  - Nirmus lineolatus var. atrimarginatus.
- Larus delewarensis.
  - Docophorus lari.
  - Nirmus punctatus.
  - Menopon infrequens.
- Larus brachyrhynchus.
  - Nirmus lineolatus var. atrimarginatus.
- Larus canus.
  - Nirmus lineolatus var. atrimarginatus.
- Larus heermanni.
  - Docophorus lari.
  - Colpocephalum funebre.
- Sterna maxima.
  - Docophorus melanocephalus.
- Diomedea albatrus.
  - Nirmus giganticola.
  - Lipeurus diversus.
    - densus.
    - concinnus.
    - ferox.
  - Giebelia mirabilis.
  - Eurymetopus taurus.
  - Colpocephalum pingue.
  - Menopon irrumpens.
- Fulmarus glacialis glupischa
  - Nirmus maritimus.
- Puffinus creatopus.
  - Lipeurus diversus.
    - testaceous.
    - fuliginosus var. major.
    - laculatus.
  - Giebelia mirabilis.
  - Menopon paululum.
- Puffinus opisthomelas.
  - Docophorus validus.
  - Lipeurus diversus
    - testaceous.
    - limitatus.
    - fuliginosus var. major.
  - Ancistrona gigas.
  - Giebelia mirabilis.
  - Menopon paululum.

- Puffinus griseus.
  - Nirmus giganticola.
    - pacificus.
  - Lipeurus diversus.
    - limitatus.
  - Giebelia mirabilis.
  - Ancistrona gigas.
  - Menopon paululum.
    - petulans.

- Puffinus tenuirostris.
  - Lipeurus diversus.
    - limitatus.
  - Giebelia mirabilis.
- Puffinus bulleri.
  - Lipeurus diversus.
    - limitatus.
  - Giebelia mirabilis
- Phalacrocorax penicillatus.
  - Lipeurus farallonii.
  - Menopon titan var. incompositum.
- Pelecanus californicus.
  - Lipeurus forficulatus.
  - Menopon titan var. linearis.
- Anas americana.
  - Trinoton luridum.
- Spatula clypeata.
  - Lipeurus squalidus.
  - Trinoton lituratum.
    - luridum.

- Aythya marila nearctica.
  - Docophorus icterodes.
  - Trinoton luridum.
- Aythya affinis.
  - Docophorus icterodes.
- Rallus obsoletus.
  - Oncophorus bisetosus var. californicus.
  - Menopon tridens.
- Rallus virginianus.
  - Oncophorus bisetosus var. californicus.
  - Menopon tridens.
- Tringa minutilla.
  - Docophorus fusiformis.
  - Nirmus complexivus.
- Calidris arenaria.
  - Nirmus actophilus.
    - complexivus.
  - Colpocephalum spinulosum var. minor.
- Limosa fedoa.
  - Nirmus cordatus.
- Squatarola squatarola.
  - Docophorus fuliginosus.
  - Nirmus incœnis.
  - Colpocephalum timidum.
- Ægialitis semipalmata.
  - Docophorus fuliginosus.
  - Nirmus opacus.
- Oreortyx pictus plumiferus.
  - Lipeurus docophoroides var. californicus.
- Dendragapus obscurus fuliginosus.
  - Lipeurus perplexus.
- Pediocætes phasianellus columbianus.
  - Lipeurus perplexus.
  - Goniodes mammillatus.
- Elanus leucurus.
  - Nirmus fuscus.
- Accipiter atricapillus striatulus.
  - Nirmus fuscus.
- Buteo borealis calurus.
  - Nirmus fuscus.
- Aquila chrysaëtos.
  - Docophorus pictus.
  - Colpocephalum flavescens.
- Haliæetus pelagicus.
  - Colpocephalum flavescens.
- Falco sparverius deserticolus.
  - Nirmus fuscus.
- Asio wilsonianus.
  - Docophorus cursor.
- Syrnium nebulosum.
  - Docophorus speotyti.
- Scotiaptex cinerea.
  - Oncophorus remotus.
- Nyctea nyctea.
  - Docophorus ceblebrachys.
- Dryobates pubescens gairdnerii.
  - Menopon funereum.
- Dryobates nuttallii.
  - Docophorus singularis.
- Xenopicus albolarvatus.
  - Docophorus californiensis.
- Sphyrapicus thyroideus.
  - Docophorus californiensis.

- Melanerpes formicivorus bairdi.
  - Docophorus californiensis.
- Trochilus alexandri.
  - Nirmus vulgatus.
- Calypte costæ.
  - Physostomum prominens.
- Tyrannus verticalis.
  - Nirmus fœdus.
- Myiarchus cinerascens.
  - Docophorus communis.
    - rufus.
    - fusco-ventralis.
  - Nirmus vulgatus.
    - fœdus.
  - Physostomum sp.
  - Menopon distinctum.
- Sayornis saya.
  - Nirmus fœdus.
  - Physostomum sp.
- Contopus richardsonii.
  - Physostomum sp.
- Empidonax difficilis.
  - Docophorus communis.
  - Nirmus vulgatus.
    - ductilis.
  - Physostomum sp. sucinaceum.
- Otocoris alpestris chrysolæma.
  - Docophorus communis.
- Cyanocitta stelleri frontalis.
  - Docophorus communis.
  - Nirmus vulgatus.
- Aphelocoma californica.
  - Docophorus communis.
  - Menopona persignatum.
- Sturnella magna neglecta.
  - Docophorus communis.
- Scolecophagus cyanocephalus.
  - Docophorus communis.
- Coccothraustes vespertinus montanus.
  - Menopon funereum.
- Carpodacus mexicanus frontalis.
  - Nirmus vulgatus.
- Spinus pinus.
  - Docophorus communis.
- Chondestes grammacus strigatus.
  - Docophorus communis.
  - Nirmus vulgatus.
  - Menopon incertum.
- Zonotrichia leucophrys intermedia.
  - Docophorus communis.
- Zonotrichia leucophrys gambelii.
  - Docophorus communis.
- Zonotrichia coronata.
  - Docophorus communis.
  - Nirmus vulgatus.
  - Menopon mæstum.
- Spizella sp.
  - Docophorus communis.
- Spizella socialis arizonæ.
  - Docophorus communis.
- Junco hyemalis oregonus.
  - Physostomum diffusum.
- Junco hyemalis thurberi.
  - Docophorus mirinotatus.
- Amphispiza belli.
  - Docophorus communis.
  - Nirmus lautiusculus.
- Melospiza fasciata heermanni.
  - Colpocephalum grandiculum.
- Melospiza fasciata samuelis.
  - Docophorus communis.
  - Physostomum sp.
  - Menopon mæstum.
- Pipilo maculatus megalonyx.
  - Nirmus vulgatus.
  - Physostomum sp.
- Pipilo fuscus crissalis.
  - Docophorus communis.
  - Nirmus vulgatus.
  - Colpocephalum grandiculum.
  - Physostomum sp.
- Zamelodia melanocephala.
  - Docophorus communis.
- Guiraca cærulea eurhyncha.
  - Docophorus communis.
  - Nirmus vulgatus.

- Passerina amœna.
  - Nirmus vulgatus..
- Piranga ludoviciana.
  - Docophorus communis.
- Petrochelidon lunifrons.
  - Menopon malleus.
- Chelidon erythrogastra.
  - Nirmus longus var. domesticus.
- Ampelis cedrorum.
  - Docophorus communis.
  - Nirmus brachythorax.
  - Physostomum sp.
- Phainopepla nitens.
  - Nirmus fœdus.
- Lanius borealis.
  - Docophorus communis.
- Lanius ludovicianus gambeli.
  - Docophorus communis.
  - Nirmus fœdus.
- Vireo solitarius plumbeus.
  - Docophorus communis.
- Vireo bellii pusillus.
  - Physostomum sp.
- Helminthophila celata lutescens.
  - Nirmus vulgatus.
- Dendroica æstiva.
  - Docophorus communis.
- Dendroica æstiva.
  - Nirmus vulgatus.
  - Menopon ridulosum.
- Icteria virens longicauda.
  - Nirmus fœdus.
- Cinclus mexicanus.
  - Nirmus vulgatus.
- Heleodytes brunneicapillus.
  - Menopon malleus.
    - distinctum.
- Thryothorus bewickii spilurus.
  - Docophorus communis.
    - mirus.
  - Menopon incertum.
- Parus inornatus.
  - Docophorus communis.
- Parus gambeli.
  - Nirmus vulgatus.
- Parus rufescens neglectus.
  - Nirmus vulgatus.
- Turdus ustulatus.
  - Menopon incertum.
- Turdus aonalaschkæ auduboni.
  - Docophorus communis.
- Sialia mexicana occidentalis.
  - Docophorus communis.
  - Nirmus vulgatus.

EXPLANATION OF PLATES.

PLATE V.—Fig. 1, *Docophorus procax* Kellogg and Chapman, ♀. Fig. 2, *D. validus* Kellogg and Chapman, ♀. Fig. 3, *D. fusiformis* Denny, ♂. Fig. 4, *D. pictus* Giebel, ♀. Fig. 5, *D. singularis* Kellogg and Chapman, ♀. Fig. 6, *D. mirinotatus* Kellogg and Chapman, ♀. Fig. 7, *D. mirus* Kellogg and Chapman, ♀. Fig. 8, *Nirmus pacificus* Kellogg and Chapman, ♀. Fig. 9, *N. fusco-marginatus* Denny, var. *americanus* Kellogg and Chapman, ♀.

PLATE VI.—Fig. 1, *Nirmus maritimus* Kellogg and Chapman, ♀. Fig. 2, *N. triangulatus* Nitzsch, ♀. Fig. 3, *N. complexivus* Kellogg and Chapman, ♀. Fig. 4, *N. actophilus* Kellogg and Chapman, ♀. Fig. 5, *N. incœnis* Kellogg and Chapman, ♀. Fig. 6, *N. opacus* Kellogg and Chapman, ♀. Fig. 7, *N. fœdus* Kellogg and Chapman, ♀. Fig. 8, *N. ductilis* Kellogg and Chapman, ♀. Fig. 9, *N. lautiusculus* Kellogg and Chapman, ♂.

PLATE VII.—Fig. 1, *Lipeurus laculatus* Kellogg and Chapman, ♂. Fig. 2, *L. concinnus* Kellogg and Chapman, ♂. Fig. 3, *L. fuliginosus* Taschenberg, var. *major* Kellogg and Chapman, ♂. Fig. 4, *L. faralloni* Kellogg, ♂. Fig. 5, *L. perplexus* Kellogg and Chapman, ♀. Fig. 6, *Oncophorus bisetosus* Piaget, var. *californicus* Kellogg and Chapman, ♀. Fig. 7, *O. remotus* Kellogg and Chapman, ♂. Fig. 8, *Colpocephalum perplanum* Kellogg and Chapman, ♀. Fig. 9, *C. spinulosum* Piaget, var. *minor* Kellogg and Chapman, ♂. Fig. 10, *C. grandiculum* Kellogg and Chapman, ♀.

PLATE VIII.—Fig. 1, *Menopon irrumpens* Kellogg and Chapman, ♀. Fig. 2, *M. paululum* Kellogg and Chapman, ♀. Fig. 3, *M. petulans* Kellogg and Chapman, ♂. Fig. 4, *M. titan* Piaget, var. *incompositum* Kellogg and Chapman, dorsal aspect of one abdominal segment. Fig. 5, *M. titan* Piaget, var. *incompositum* Kellogg and Chapman, ventral aspect of last segments of abdomen of ♂. Fig. 6, *M. funereum* Kellogg and Chapman, ♂. Fig. 7, *M. distinctum* Kellogg and Chapman, ♀.

PLATE IX.—Fig. 1, *Menopon persignatum* Kellogg and Chapman, ♀. Fig. 2, *M. mœstum* Kellogg and Chapman, ♀. Fig. 3, *M. malleus* Nitzsch, ♀. Fig. 4, *M. ridulosum* Kellogg and Chapman, ♀. Fig. 5, *Physostomum prominens* Kellogg and Chapman.

Oc. Papers, Cal. Acad. Sci. Vol. VI. [Kellogg & Chapman] Plate V.

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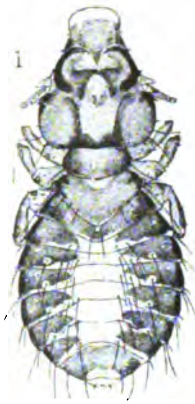

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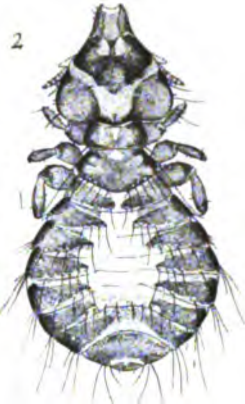

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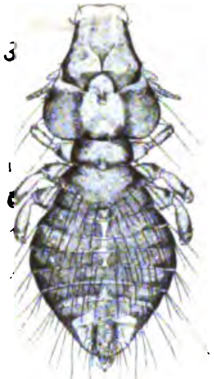

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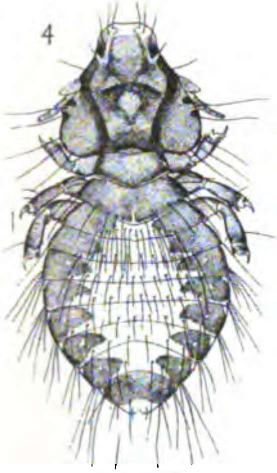

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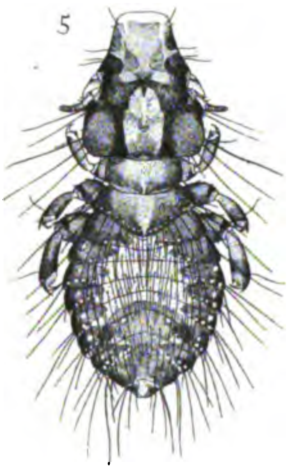

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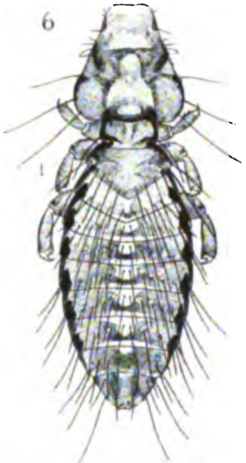

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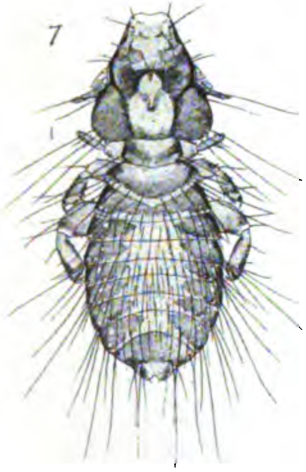

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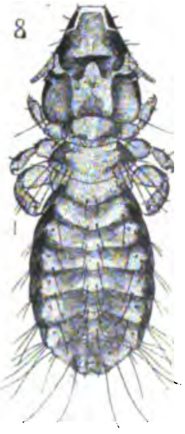

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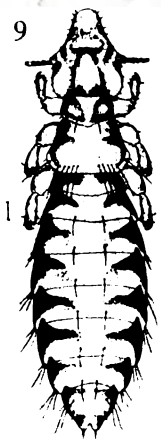

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Oc. Papers, Cal. Acad. Sci. Vol. VI. [Kellogg & Chapman] Plate VI.

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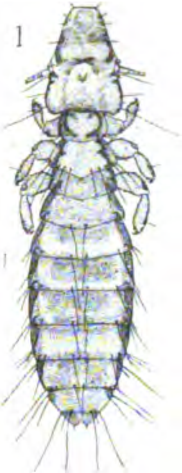

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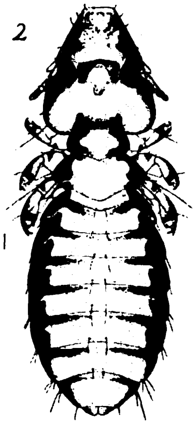

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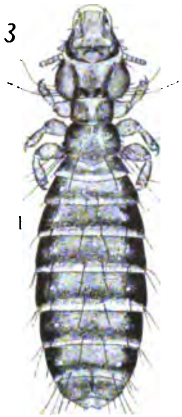

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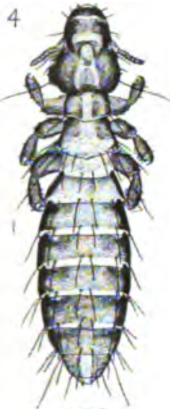

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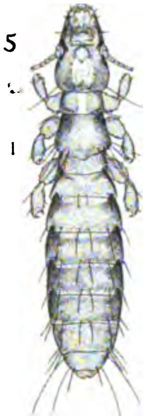

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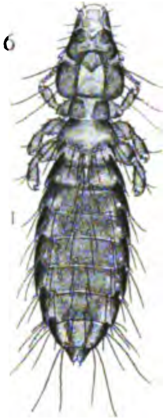

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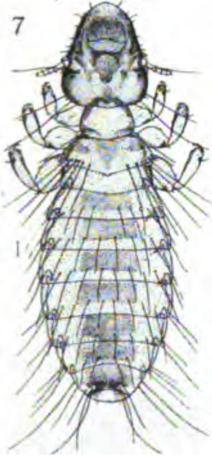

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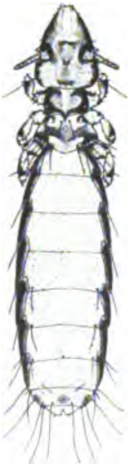

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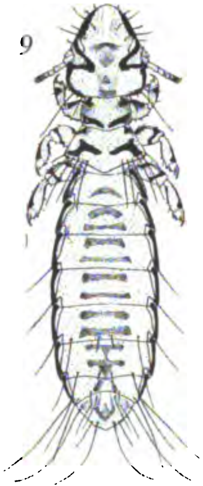

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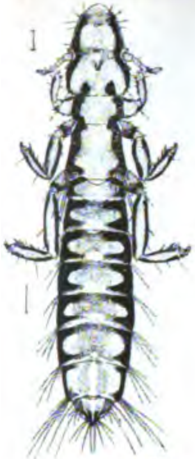

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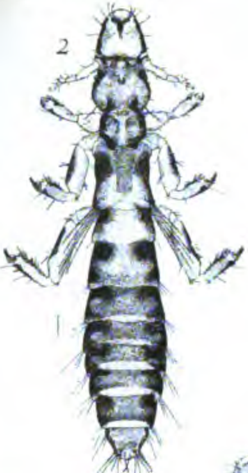

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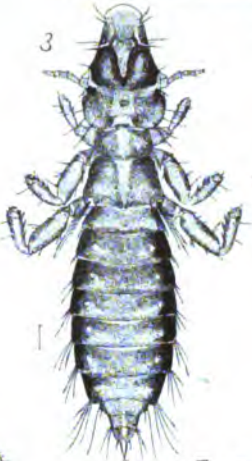

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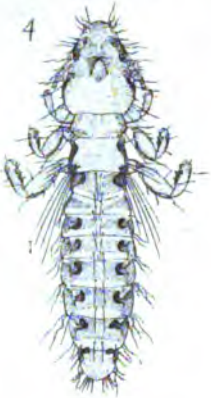

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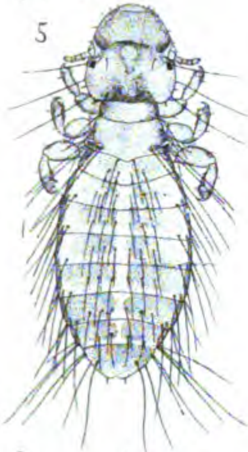

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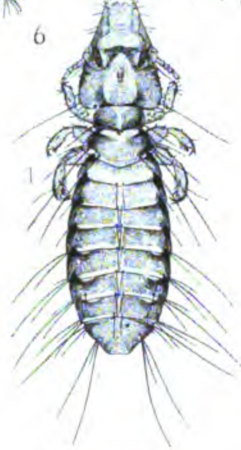

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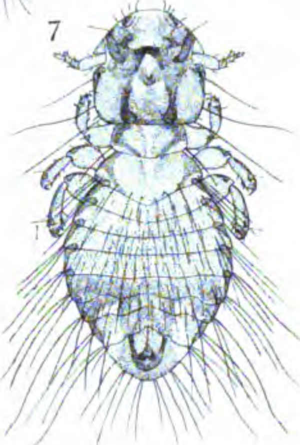

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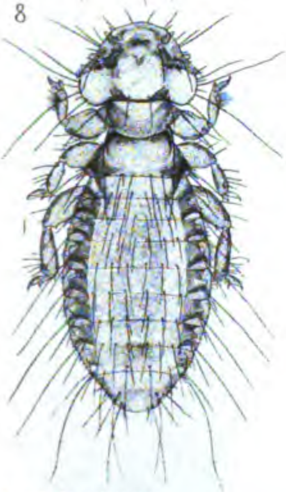

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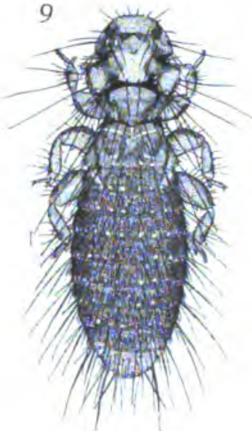

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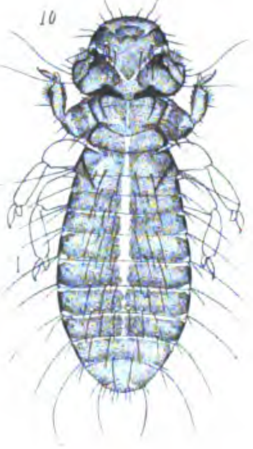

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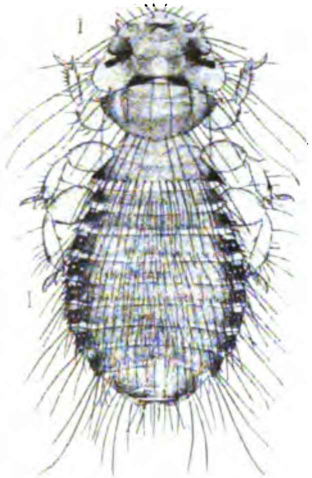

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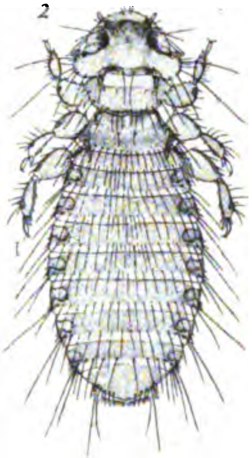

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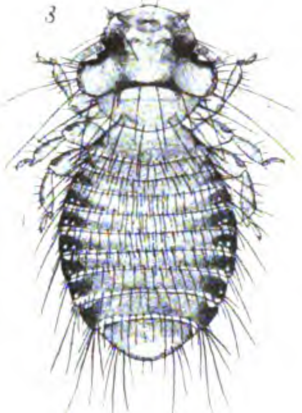

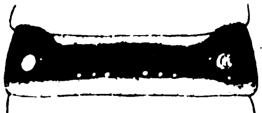

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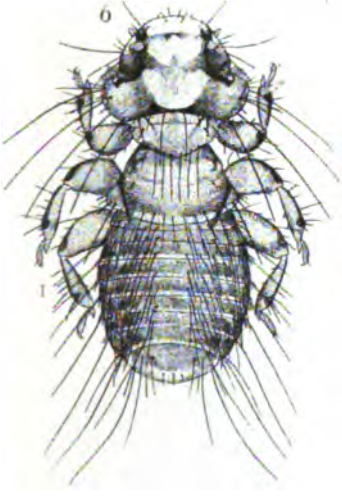

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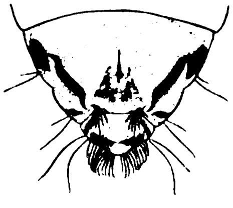

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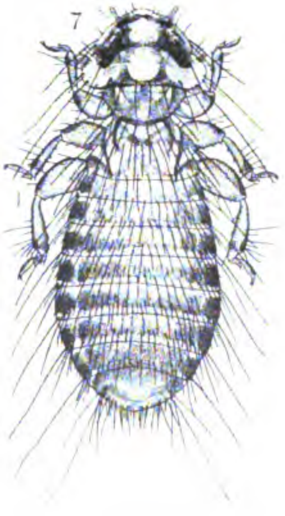

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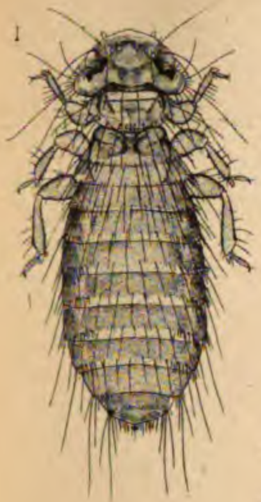

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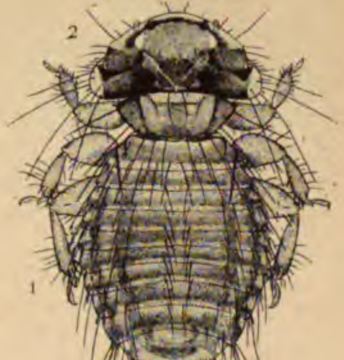

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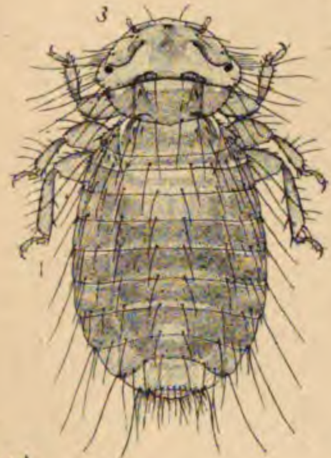

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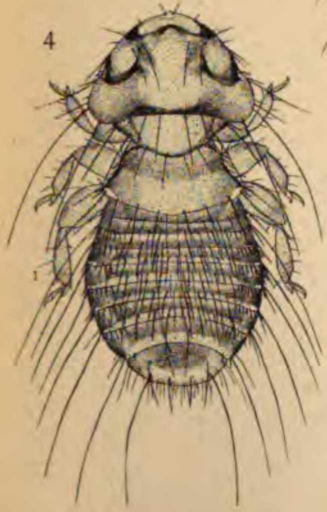

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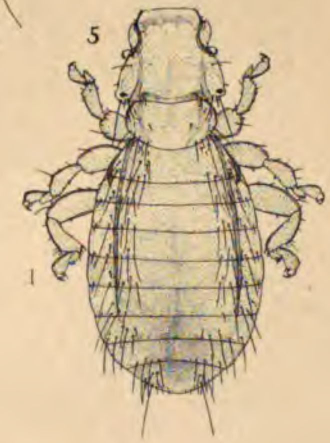

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THE ANATOMY OF THE MALLOPHAGA.

(With Plates X to XVII.)

BY ROBERT E. SNODGRASS.

The earliest work on the anatomy of the Mallophaga is that of Nitzsch. His results are comprised in his own announcement of his work, "Darstellung der Familien und Gattungen der Thierinsekten (insecta epizoica) als Prodromus einer Naturgeschichte derselben," published in the third volume of Germar and Zinken's "Magazin für die Entomologie," 1818, and in Giebel's "Insecta Epizoa, die auf Säugethieren und Vögeln schmarotzenden Insecten, nach Chr. L. Nitzsch's Nachlass bearbeitet," published in 1874. Both of these works are chiefly systematic, but the larger groups are separated on anatomical characters. The first purely anatomical paper is one by Wedl in 1855, "Ueber das Herz von *Menopon pallidum.*" This paper is limited to a single organ. The next, by Kramer, "Beiträge zur Anatomie und Physiologie der Gattung *Philopterus* (Nitzsch)," published in Zeitschrift für Zoologie in 1869, includes all the organs of a single species (*Lipeurus jejunus*). The third and latest purely anatomical paper is Grosse's "Beiträge zur Kenntnis der Mallophagen," published in the same journal as the last, in 1885. *Menopon titan* (*Tetrophthalmus chilensis* Grosse), is made the basis for detailed descriptions, but the work is comparative, since more general descriptions of other forms are given, and the anatomical characters of the two main groups are pointed out. In 1869 Rudow published a paper, "Beobachtungen über die Lebensweise und der Bau der Mallophagen oder Pelzfresser, sowie Beschreibung neuer Arten," in which the

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principal anatomical characters are tabulated, and a long description of the mouth-parts given. The latter, however, is almost entirely incorrect. The mouth-parts were described wrongly at first by Nitzsch, then by Kramer, and finally by Rudow. Their correct explanation is due to Grosse. Rudow's paper contains an important statement concerning the number of egg-tubules in *Amblyceran* females. He says that there are five present of which two are rudimentary. Nitzsch could find but three, and Grosse apparently made no determination of the number present. In 1869, also, Melnikow published in Archiv für Naturgeschichte, vol. xxxv, an embryological paper, "Beiträge zur Embryonal-entwicklung der Insekten" in which the embryology of the Mallophaga is described. Nusbaum in his paper, "Zur Entwicklungsgeschichte der Ausführungsgänge der Sexualdrüsen bei den Insekten," in Zoologischer Anzeiger for 1882, describes mainly two Mallophagan species, *Lipeurus bacillus* and *Goniocotes hologaster*.

I. General External Anatomy.

External Form and Body-wall.—The body is generally very much flattened dorsoventrally. The segments of the thorax are often apparently only two, the mesonotum and metanotum being united. In others, however, the two are distinct although the former is narrow. In longitudinal sections of *Menopon titan* (plate x, fig. 1), the mesonotum (T_2) is seen to be separated from the metanotum (T_3) by a non-chitinized space, and is depressed below the level of the latter. The number of abdominal segments varies, but the largest is ten. The number in some cases varies with the sex. The head is flat, horizontal, situated closely upon the prothorax, and often excavated behind to receive the latter. In *Menopon persignatum*, as shown by transverse sections (plate xii), the head is very flat and comparatively wide. The side walls are very far from being perpendicular, and are scarcely distinguishable from the dorsal walls. They meet the floor of the cranium at a sharp angle. The top of the head is flat in front, somewhat concave behind. The prothorax is triangular in cross-section, having one angle median and ventral. The tergum is a little rounded. The mesothorax is more convex above and flatter beneath. The lateral edges are sharp and project over the bases of the legs. The metathorax is wider but otherwise similar to the mesothorax except in length. In the females of some species the abdomen is little or not at all flattened.

The body-wall of most species is well chitinized. In the abdomen the chitin is deposited in several areas around each segment (plate xv, figs. 3, 4, and 5, and plate xvii, figs. 1–5). On the dorsal side is a wide continuous plate reaching on each side to a short distance from the lateral margin of the segment. Likewise on the ventral side is a similar chitinization, and the two plates form respectively the tergum and sternum of the segment. Laterally, between the outer ends of these, are angular plates, one on each side, forming the lateral walls or pleura of the segment. The four are separated from one another by non-chitinized spaces. The intersegmental spaces are generally, especially on the dorsum, thrown into S-shaped folds, so that the posterior end of one segment overlaps the anterior end of the one in front. In some cases the chitinous tergum or sternum of a segment occupies only a small part of its length. In some the chitin is mostly accumulated at one place. An extreme example is shown in the terga of the anterior abdominal segments of *Eurymetopus taurus.* Here the chitin shows in longitudinal sections a large oval thickening near the anterior end of the segment, back of which it forms only a thin superficial plate reaching to near the posterior end. Anteriorly it terminates in a deeper but very short prolongation. The non-chitinized part in front is folded into a strong S-shaped band, the upper loop of which, forming the posterior border of the segment in front, projects over the anterior end of the chitinous thickening. Processes of the chitinous wall often extend into the body-cavity, especially in the thorax, giving attachment to various muscles. The antennary fossæ of the Amblycera are formed by chitinous processes from the lateral ventral margins of the head extending outward beneath the antennæ, and by a prolongation of the outer dorsal aspects of the head outward and downward (plate xii, figs. 1 and 2). Chitinous genital parts will be described under the head of the Reproductive Organs.

The Appendages.—The antennæ are three to five-jointed. In the Amblycera they are concealed in deep fossæ on the lateral ventral aspects of the head, and generally have the terminal segment enlarged. In the Ischnocera they are simple, filiform and exposed.

The mouth-parts have already been described in detail in Kellogg's "New Mallophaga, II,"* and merely a general account of their structure will be given here. They are of the biting type and consist of mandibles, maxillæ, and labium. The maxillæ (plate x, figs. 5, 6, 11 and 12) are large, strong, triangular, two-toothed structures, attached to the head by a condyle on one side and a socket on the opposite side of the outer basal angle. From the inner angle of the base a prolongation extends inward. The two teeth project from the inner edge, generally one distal to the other. The mandibles present two modifications, one found in the Amblycera and the other in the Ischnocera. In the former they lie parallel with the ventral surface of the head, so that the condyle is ventral and the socket dorsal. In this form one tooth lies in front of the other in a horizontal line in the same plane as the long axis of the mandible. In the Ischnocera the mandibles hang vertical to the head, so that the condyle is posterior and the socket anterior. In this form the distal tooth is typically ventral to the other in a vertical line in the same plane as the long axis of the mandible. The more proximal tooth, however, may be moved toward the tip and come to lie by the other and in front of it (plate x, fig. 6). In this case the two lie in the same horizontal line, but this is perpendicular to the long axis of the mandible. Starting with either type, the other may be produced from it by revolving the mandible on an axis passing from its outer to its inner basal angles. The degree of revolution varies in different Ischnoceran species, but the angle is always large and may reach 90°. In many cases there is a chitinous plate or rod attached to the inner angle of the base of the mandible, and a smaller one attached to the outer. These serve for attachment of muscles (plate x, fig. 12, *ch. pls.*) extending backward or upward into the head cavity. When they are absent muscle fibers are attached directly to the mandibles.

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* Proc. Cal. Acad. Sci., 2nd Ser., Vol. VI, 1896.

The maxillæ are generally simple, small, non-chitinized lobes, often provided with teeth on their inner edges. They lack palpi and distinct divisions into the ordinary parts (plate x, figs. 3 and 10).

The labium presents two forms, one in the Amblycera the other in the Ischnocera. In the former (plate x, fig. 9), there are present a submentum, mentum with two four- segmented palpi, and a ligula with two glossæ and two paraglossæ. The ligula is the only part that varies much, since it may have more or fewer than the four lobes named. In the Ischnocera a submentum, mentum, and ligula are present. The latter two are not well separated, but the paraglossæ are distinct (plate x, fig. 13) and very constant in form, being short, thick, cylindrical, and rather more chitinized than the rest of the labium. The glossæ are present between the paraglossæ as two small lobes.

In front of the mouth is the labrum, a large lobe situated on the ventral aspect of the head, generally some distance back of the anterior border of the clypeus.

The three pairs of legs are very similar throughout the group. The tarsi are two-jointed, and, with the exception of two genera, *Trichodectes* and *Gyropus*, that inhabit mammals, are provided with two claws, the others having only one. In some specimens of *Docophorus cursor* examined, the legs when at rest generally assumed the following positions. The femur (fig. 1) of the metathoracic leg extends outward and is inclined slightly forward

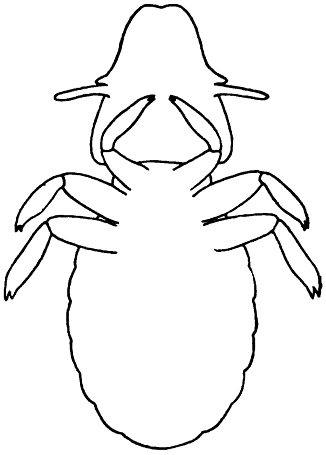

Fig. 1.

from the body. The femur of the mesothoracic leg extends outward also but a little more forward than the other. That of the prothoracic leg is inclined forward at an angle of about 45° with the body. Hence the fore legs are held mostly beneath the head and anterior part of the prothorax. The meta- and mesotibiæ extend backward, outward, and downward from the distal ends of the corresponding femora. The protibiæ extend backward, inward, and downward from the distal ends of the profemora, and their distal ends lie internal to the coxal ends of the femora.

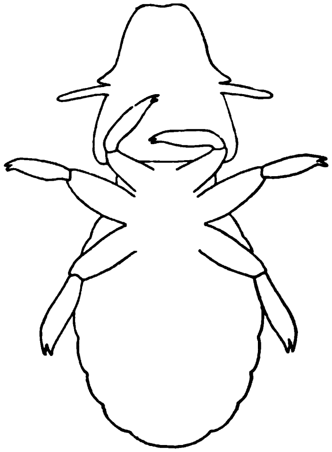

Fig. 2.

When the insect is walking undisturbed in forward longitudinal progression, the two legs of the mesothorax and of the metathorax move respectively together, but the two pairs move in opposite directions. That is (figs. 2 and 3), the two mesothoracic legs move forward or backward at the same time and the metathoracic legs move in the same manner, but while the mesothoracic legs are moving forward, the metathoracic legs are moving backward, and *vice versa*. Thus, while one pair of legs is pushing the body forward the other pair is reaching forward for a new grasp, and this is obtained just as the active pair has finished its work. The pair previously being carried forward then takes hold and continues the motion of the body, the two being themselves brought relatively backward. In this way the two pairs are always either approaching each other or are receding from each other.

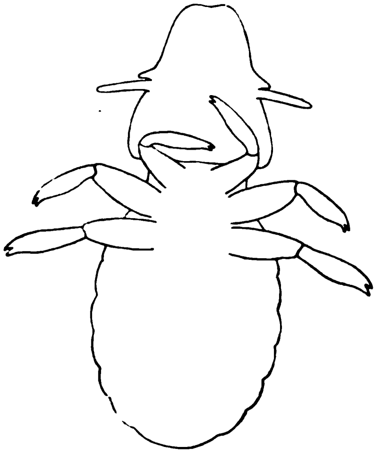

Fig. 3.

The prothoracic legs do not move synchronously with either of the other pairs nor with each other. Generally (fig. 3) one moves backwards while the other is reaching forward. They appear mainly to guide the body. The femoro-tibial joint is most of the time in front of the tarsal claws, so that their power as propellers cannot be great. The parasite thus progresses along the feather with a hand over hand movement of the prothoracic legs, as of a man climbing a rope, while the other legs, a pair at a time, are continually pushing the body forward.

This is the typical movement of the legs and the one which prevails when the insects are walking quietly and regularly, but at times it becomes very much obscured by irregular movements and is generally more or less so, so that almost any relative position of the legs may be seen. The outer end of the metathoracic femur is seldom brought much farther forward than its coxa. The mesothoracic femur forms a smaller angle with the body in front, but not such a small one behind as the metathoracic leg. The femoro-tibial joints of the prothoracic legs are during progression brought forward, and the tibia also independently turns forward on the femur, so that the angle between the two increases and the tarsal claws are carried forward by a double motion. They then grasp the feather and by their own motion backward and by the motion of the body forward on the hind legs the femoro-tibial angle is again decreased and the leg assumes its former position. The insects run along on the feathers very easily, generally preferring the shaft. Those experimented with were kept on a few bits of feather on a glass slide. They ran along the shaft of a feather until they came to the end, then backed up a short distance, turned around, and ran back to the other end to go through the same performance there. They generally move with the head forward but can apparently go backwards or at any lateral angle just as easily; they nearly always, however, turn around when they wish to reverse the direction of movement. When several were placed on some guinea-pig hairs they appeared to be at no loss at all as to how to get along, and traveled just as well as on the feathers, although perhaps a little slower. Some Pediculids, however, from the guinea-pig, when placed on some feathers, appeared to be somewhat hindered by the network of barbs and barbules. The Mallophaga were entirely unable to progress upon the glass slide when they got off of the feathers, but the lice showed no difficulty at all in this respect; the latter could also right themselves when placed on their backs while the former could not.

II. The Alimentary Canal and its Appendages.

The Alimentary Canal.—The alimentary canal presents two types of structure. One form is simple, having no special development at any part, the other is complicated by a lateral and backward prolongation of the crop, so that the latter forms a large expanded diverticulum of the œsophagus. The first form is confined to the Amblycera, the second to the Ischnocera. Of the first, the alimentary canal of *Menopon titan* (plate xi, fig. 13, plate x, fig. 1, and plate xvii, fig. 6) may be taken as an example. It has the form of an almost straight tube separable into six distinct parts. The first of these is a narrow elongated buccal cavity (plate x, fig. 1, *bc*) extending upward and backward from the oval aperture, by which it opens anteriorly, to the second part of the alimentary canal, the pharynx (*p*). This is a large cavity, oval in longitudinal sections, having its long axis extending backward and upward, but not so much in the latter direction as that of the buccal cavity, so that the two form an angle with each other. The pharynx lies mostly in front of the brain (*b*) and subœsophageal ganglion (*s.œ. g.*), the commisures lying laterad of its posterior end. Between the latter the pharynx contracts and passes into the œsophagus. This is rather long, narrow, gradually expands posteriorly, passes uninterruptedly into the crop, and forms with the latter the third division of the alimentary canal (*œ* and *cr*). The crop is of variable size according to the contents, but is rather large when distended.

The fourth part, the ventriculus, is long, wide in front and narrow behind, and connected with the crop in front by a short, very narrow neck. On each side of this it is produced into a large cæcum, the two embracing the posterior end of the crop. Back of the stomach is the intestine forming the fifth and sixth divisions of the alimentary tract. The first of these two consists of the prerectal part of the intestine and the second of rectum. The former is a short, straight, narrow tube, a little enlarged toward the middle and separated from the ventriculus in front and the rectum behind by slight constrictions. From its anterior end four Malpighian tubules arise. The rectum is very large (plate xi, fig. 13, and plate xvii, fig. 6, *r*). Its anterior part is much dilated, the enlargement being rather suddenly narrowed in front, but posteriorly gradually passes into the more tubular posterior part. Its anterior end is provided with six oval rectal glands. These vary in size in different specimens. In the male the anal opening is in the upper posterior part of the genital chamber, in the female it is in the end of the last abdominal segment (plate xv, figs. 1 and 2, *a*, and plate xvii, fig. 6, *a*).

Sections show the following histological features of the alimentary canal. The preventricular part is lined with a chitinous intima continuous with the body-covering at the mouth. The ventriculus lacks an intima, but possesses a thick inner cellular epithelium (plate x, fig. 1, *v*). The intestine has a thin chitinous lining continuous with the body-covering at the anus. The prerectal part possesses a thin cellular epithelium covered by an outer membrane, surrounding which are small muscle fibers. The rectum lacks the epithelium and has larger muscle fibers (plate xvii, fig. 6, *rtm*). The rectal glands project inwardly and are covered by the chitinous lining of this part of the alimentary tract.

In the Ischnocera, as before stated, the alimentary canal is complicated by a very remarkable condition of the crop. This in the genus *Trichodectes* has the form of a large sac connected with the lower end of the œsophagus by a long, narrow neck; in the other genera it forms a large transverse dilatation of the œsophagus, some distance above where the latter opens into the ventriculus. The crop is always produced much more to one side of the œsophagus than to the other.

The alimentary canal of *Eurymetopus taurus* may be taken as a type of this latter form (plate xi, fig. 11). The œsophagus is a long, slender tube reaching from the head to the mesothorax. Here it enters the anterior dorsal aspect of the crop. The latter lies dorsal and to the left of the other organs of the body-cavity except the heart, and extends from the middle line backwards and to the left, reaching the sixth abdominal segment when considerably distended. Its size and shape vary according to its contents, but it is generally much longer than wide, rounded in front, swollen toward the middle, and tapering behind. Its upper end extends a short distance beyond the opening of the œsophagus into it. About opposite the latter point, on the ventral aspect of the crop, the subingluvial part of the œsophagus begins and runs backwards to the ventriculus, forming a short, narrow tube. The ventriculus is smaller than the crop when the latter is fully distended. Anteriorly it bears two large, lobular cæca, each being rather flat and expanded beyond its base. The stomach lies with most of its long axis in an antero-posterior direction. It is widest through the middle; in front of this it is slightly constricted, while in the opposite direction it becomes very much narrowed, and, assuming a tubular form, makes a bend to the left. It goes a short distance in this direction and then meets the hind-gut. The latter turns immediately backward and runs in a straight line to the exterior. It is divided into an anterior, narrow, prerectal part and a posterior, enlarged rectum. The former bears at its anterior end the four Malpighian tubules, becomes enlarged toward its middle, and is separated posteriorly from the rectum by a slight constriction. The latter is much distended in front, where six large, oval, rectal glands are situated, but becomes narrowed posteriorly, the hind half being a straight, narrow tube opening into the upper part of the genital cavity. The relative size and shape of each of these parts vary greatly with their contents. The crop is provided with very prominent longitudinal and transverse muscles, which form a network of fibers over it.

It is evident that in such an alimentary canal as that just described there are two distinct divisions in addition to those of the alimentary canal of an Amblyceran species. The crop of *Eurymetopus* forms a part distinct and sharply separated from the œsophagus in front, and also sets off that portion of the œsophagus between itself and the stomach as a distinct division of the alimentary tract. The bits of feathers that form the food of the insect are generally almost as long as the crop and always lie in it in a longitudinal direction.

The alimentary canals of all other Philopterids in which this organ is known are similar in all essential respects to that of *Eurymetopus taurus* just described. In *Docophorus lari* the crop is very much like that of *Eurymetopus taurus* in shape (plate xi, fig. 8). It extends from the anterior left part of the body-cavity backwards and to the right. The œsophagus is narrow, lies in the middle line, and enters the crop some distance to the right of the anterior end of the latter. Arising from the ventral surface of the crop, at a point some distance to the left of the opening of the anterior part of the œsophagus into the same, is the subingluvial part of the œsophagus, which passes backwards a short distance and enters the ventriculus. This is rather long and tapers very much posteriorly. Its anterior end is provided with a large, lobe-like cæcum on each side. Its posterior end is a little bent just before it enters the hind-gut. The latter is short and narrow. The rectum is very much expanded anteriorly, having six prominent rectal glands surrounding the posterior end of the anterior smaller part of the intestine.

In *Goniodes cervinicornis* the crop is relatively very long and tapering (plate xi, fig. 12). It lies in an almost antero-posterior direction to the left of the rest of the alimentary canal. Its anterior end is large and rounded; posteriorly it tapers to a rather pointed extremity which reaches a little farther back than the posterior end of the ventriculus. When in the natural position its hind end is bent to the right and lies close to the stomach. The œsophagus enters the crop on its dorsal surface back of the anterior end. The part of the œsophagus between the crop and the stomach arises from the former in front of the point at which the anterior portion of the œsophagus opens into it. The stomach is rather long, but when it is distended it does not taper very much posteriorly, passing into the intestine by a rather sudden constriction. The two cæca at its anterior ends are relatively smaller than in the other forms described, and are merely blunt diverticula of the ventriculus without constricted bases. The prerectal part of the intestine is very short and narrow. The rectum on the other hand is unusually large, having its anterior end very greatly dilated and provided with six very large and much elongated rectal glands.

In *Lipeurus fuliginosus major* the crop lies to the left side of the body-cavity, the rest of the canal lying along the right. The ventriculus simply contracts posteriorly, passing gradually into the intestine, the two being separated by only a slight constriction. The rectum is comparatively rather long but otherwise both it and the rest of the intestine are very similar to the others described.

Nitzsch (1874) figures the alimentary canals of the following Philopterid species: *Docophorus fuscicollis*, *D. ocellatus*, and *Lipeurus jejunus*. That of *Docophorus fuscicollis* differs in no essential respect from those forms already described. In *D. ocellatus* the openings of the pre- and postingluvial divisions of the œsophagus are rather far removed from the nearer end of the crop. The ventriculus is very long and bent upon itself, forming a loop.

The genus *Trichodectes* (family Trichodectidæ) presents a rather remarkable deviation from the other Ischnoceran forms in the shape and position of the crop. As already mentioned, it is of the form of a sack connected with the œsophagus some distance in front of the ventriculus by a narrow, more or less elongated neck. In *Trichodectes geomydis* (plate xi, fig. 10), the crop is rather smaller comparatively than in most of the Philopterid forms, being about two-thirds the length of the stomach. The neck is long and slender, extending laterally from the œsophagus. The ventriculus is large anteriorly, where it is produced into two large cæca which are not constricted at their bases. Posteriorly the stomach becomes narrowed and makes an abrupt bend in the direction of the crop. After running a short distance in this direction as a narrow tube it passes into the intestine. This division of the alimentary canal goes backward from the midgut, forming a right angle with the posterior tubular part of the latter. The rectum is wide anteriorly, where it presents six glands as in the other families. In a *Trichodectes* from a horse the crop (plate xi, fig. 9) is the same as in *T. geomydis*, but is comparatively even a little smaller;

also, the neck is shorter. The ventriculus with its large gastric cæca is about the same. Nitzsch (1874) figures the alimentary canal of *T. climax*. Here the crop differs somewhat from the two just described in that the neck is very much shorter, the crop forming a pear-shaped diverticulum from the side of the œsophagus and separated from it by a narrow constriction. In this form the distal end of the crop is the larger, while in the Philopterid forms the proximal end is the larger, the distal end being generally more or less tapering and pointed. No intermediate form of a crop between the Philopterid and Trichodectid types has been found, and it is impossible to say which is the more primitive.

Pharyngeal Sclerite.—In many genera, including all of those of the Ischnocera, and one and part of another genus in the Amblycera, there is present a curiously formed sclerite in the walls of the pharynx. It has already been described in Kellogg's "New Mallophaga, II," under the term "œsophageal sclerite." As shown there, it is a prominent, cup-shaped thickening of the chitinous lining of the ventral wall of the pharynx, forming a depression in the latter. From its sides (plate x, fig. 7) chitinous bands (*bs*) run upward around the pharynx and are connected by muscles with the dorsal wall of the head. From the anterior corners a large expansion (*ant. h*) on each side reaches forward and upward in the walls of the pharynx. Into the anterior end of its cavity a duct from two ventrally situated glands opens. The latter (plate x, fig. 2, *l.g.*) are oval, covered with a chitinous envelope, and supported by chitinous pedicles. From the anterior end of each a duct runs forward, after traversing the ventral surface, and then turns inward and backward to unite with the duct from the other side. The common duct thus formed then goes straight back to the sclerite. The shape of both these organs is very remarkably constant. In one or two genera they present deviations, and also in a few scattered cases, but these will be described farther on.

As was pointed out by Kellogg (1896), these organs are not peculiar to the Mallophaga but occur also in the Psocidæ, having been described for these insects by Burgess (1878). Outside of these two groups, however, they are not known to occur. Among the Mallophaga they are not of universal occurrence, but are for the most part confined to one suborder. Specimens of the following genera were had for examination: *Ancistrona*, *Colpocephalum*, *Docophorus*, *Eurymetopus*, *Giebelia*, *Goniocotes*, *Goniodes*, *Læmobothrium*, *Lipeurus*, *Menopon*, *Nirmus*, *Nitzschia*, *Oncophorus*, *Physostomum*, *Trichodectes*, *Trinoton*. The following table shows the distribution of the sclerite and glands among these genera:

Genera with Sclerite and Glands Present.	Genera with Sclerite and Glands Absent.	Genera with Sclerite and Glands Present or Absent.
Colpocephalum.	*Ancistrona.*	*Docophorus.*
Eurymetopus.	*Læmobothrium.*	*Lipeurus.*
Giebelia.	*Nitzschia.*	*Menopon.*
Goniocotes.	*Physostomum.*	*Nirmus.*
Goniodes.	*Trinoton.*	
Oncophorus.		
Trichodectes.		

The above table shows that those genera with the structures present belong, with the exception of *Colpocephalum*, to the suborder Ischnocera; while those in which they are absent belong, without exception, to the suborder Amblycera. Hence there are no Ischnoceran genera in which the sclerite and glands are absent in all species, although in three genera they are absent in a few cases. On the other hand, in the Amblycera they are absent in all but two genera, and of these one has them present in all species, but in the other they may be present or may be absent. Of thirty-eight species of *Docophorus*, twenty-six species of *Lipeurus*, and twenty-nine species of *Nirmus* examined—all that were accessible—only in *Docophorus icterodes*, *Lipeurus picturatus*, *L. longipilus*, and *Nirmus signatus* are the structures absent. From this it is evident that the exceptions to the occurrence of the œsophageal sclerite and glands in North American Ischnocera are few. It is worthy of notice also that the species of this suborder lacking them occur in the three largest genera,—the species of *Docophorus*, *Lipeurus*, and *Nirmus* being far more numerous than those of all the other genera of the same suborder together.

The following genera have been found so far only on European birds, *Akidoproctus*, *Boopia*, *Bothriometopus*, *Eureum*, and *Ornithobius*. Taschenberg (1882) and Piaget (1880), however, give good figures of all these genera, and in their figures the presence or absence of the sclerite is apparently intended to be shown, although whether it is or is not present is not stated in the description of each species. The figures can probably be relied on to show at least in what species it is present. According to them the structure is present only in *Akidoproctus*. This genus and also *Bothriometopus* and *Ornithobius* belong to the Ischnocera, so that it appears that there are two genera of this suborder in which the sclerite is absent; but this is without proof. If it is absent in the two Amblyceran genera, *Boopia* and *Eureum*, they agree with most of the other forms of their suborder. The sclerite appears to be absent also in *Gyropus*, an Amblyceran mammal-infesting genus*

In some species of several genera the sclerite is not of the typical form described. In *Docophorus pertusus* it is very much modified in form. The body is comparatively very small and the anterior processes are not present at all. On the other hand, the lateral circumœsophageal bands are greatly enlarged, forming a thick chitinous band passing upward around the pharynx. The body of the structure is so small that it appears merely as a median, backward-projecting enlargement of the rest. The dorsal cavity is present, its anterior wall and the anterior margins of the lateral wings are transparent and continuous with one another. The wings are expanded near their bases but distally each becomes narrowed and passes upward and somewhat forward as a slender curved rod. The structure is of about the same shape in a young specimen but the wings are proportionally smaller. In *Docophorus atricolor* the sclerite is small and weakly chitinized but the anterior processes are comparatively large and much expanded. In *Lipeurus diversus* the body is elongated, and in *L. squalidus* it is similar but with the anterior processes enlarged. In several other Ischnoceran genera the sclerite is variously modified, but the species in which modification occurs are scattered and not closely related to one another.

In the Amblycera only two genera possess the pharyngeal sclerite, and in these two the characteristic form is not that of the Ischnocera. It is, however, typically the

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*Taschenberg figures *Bothriometopus macrocnemis*, ♂ and head of ♀, and *Ornithobius hexophthalmus*, ♀ and head of ♂, in which the sclerite is not shown. But in *Akidoproctus rostratus* and *A. stenopygos* it is plainly present. Piaget figures *Boopia longitarsus*, *B. grandis*, *Eureum cimicoides*, *E. malleus*, *Gyropus ovalis*, *G. gracilis*, and *G. turbinalis*, in all of which the sclerite is not shown.

same. In *Menopon* and *Colpocephalum* the anterior processes of the sclerite are very much prolonged forward and are only slightly divergent. In some cases the sclerite is extremely reduced in size. In *Menopon fœdus* the anterior processes are not prolonged but are wide and bifid. These two genera are in other respects also very similar, and it is of significance that in the only genera of the Amblycera that possess the sclerite it has the same structure, different from that prevailing amongst the Ischnoceran genera, in each.

The following table gives the species of *Menopon* examined that have and do not have the sclerite and glands:

Genus *Menopon*.

Species with Sclerite and Glands Present.	Species with Sclerite and Glands Absent.
auro-fasciatum	*distinctum*
decoratum	*malleus*
dissimile	*persignatum*
fœdus	*præcursor*
funereum	*rediculosum*
incertum	*robustum*
indistinctum	*titan*
infrequens	*tridens*
irrumpens	
longicephalum	
loomisii	
melanorum	
mesoleucum	
monostœchum	
navigans	
numerosum	
paululum	
petulans	
striatum	

It is evident that the œsophageal sclerite and connected glands might be made use of in determining the relations of *Menopon* and *Colpocephalum* to the other genera, and also of the Mallophaga to other orders of Insects, since they occur also in the Psocidæ. But the probable number of yet unknown species is too great to allow of these structures being used to determine relationships of genera within the order.

The Salivary Organs.—In 1869 Kramer described the salivary glands of *Lipeurus jejunus*. In 1874 they were mentioned by Giebel in "Insecta Epizoa" from Nitzsch's notes. He gives no description of them. Finally, in 1885, Grosse gave a general account of their structure in the whole order, and a special description of those of *Tetrophthalmus chilensis* (*Menopon titan*). As far as is known, all species of Mallophaga possess two pairs of salivary organs; in some cases there is evidence that only one of each pair is a gland, the other being a reservoir. In any case either one gland and a reservoir or two glands are situated on each side of the crop or œsophagus. From the anterior end of each organ a duct arises and passes forward. The two ducts on each side unite with each other, forming a right and left common salivary duct. These run forward a varying distance and then approach each other and unite in the middle line. This final duct formed of the four primary ducts runs forward beneath the œsohpagus and enters the head where it opens into the pharynx.

In the suborder Amblycera the salivary organs appear to have no constant form characteristic of the subgroup. Grosse describes those of *Menopon titan* (plate xi, fig. 2) as consisting of a gland *(a)* and reservoir *(b)* on each side. The glands are elongate-oval, and each has a furrow on the inner side, from the middle of which the duct arises. The reservoirs are long and club-shaped, having the ducts passing forward from the anterior ends. He describes also the glands of a *Læmobothrium* as being composed of twenty small tubes situated upon the salivary duct like the teeth of a comb.

Nitzsch gives several figures showing the salivary glands. In *Menopon mesoleucum* two pairs of glands are shown of which the inner ones are very long and comparatively narrow. They extend in a straight course backwards along the sides of the alimentary canal as far as the rectal glands. In front they become narrowed and pass gradually into the ducts. External to each of these is a shorter gland. This one is also rather elongated and tapers in front and behind. The posterior end is coiled, while the anterior end passes into the duct. Grosse makes the general statement that the salivary organs consist of a salivary gland and a saliva reservoir, and that the latter are filled with a viscous substance.

In the Ischnocera the organs have a more definite shape, being much less variable among the different species. They consist of two pairs of glands and their ducts. Each pair lies on one side of the alimentary canal in the region of the anterior end of the crop and is composed of an outer, generally larger gland, and an inner, smaller one (plate xi, fig. 11, *r* and *g*). In *Trichodectes geomydis* (plate xi, fig. 1) the two are of about the same size. The inner one (*b*) has its long axis transverse and its larger end turned inwardly; while the outer is oval. The outer organ generally has the appearance of being a reservoir rather than a gland. Kramer studied the histology of the two and described the cells of the inner, smaller one as being remarkably distinct, while those of the outer he says are only with the greatest difficulty made out to be cells. He found the outer organs mostly filled with fat-like drops.

Both Kramer and Grosse describe a second set of salivary glands found only in the Ischnocera. Kramer described those of *Lipeurus jejunus* as consisting of a group of fourteen cells attached to the smaller of the two glands just described. He could find no ducts connected with them, but, since they were always present and constant in position and arrangement, he still regarded them as having a saliva-secreting function. Grosse observed them in the genera *Nirmus*, *Trichodectes*, and *Lipeurus*. He found, however, that they occurred not only on the crop but also in groups of two, six, and eight, connected with the fat body. On this account, and since he also could discover no duct in connection with then, he concluded that their function as salivary organs was very doubtful.

In *Trichodectes geomydis* there can be no doubt of this glandular nature, for here ducts can be very easily observed. If the alimentary canal be removed from the body and transferred to a glass slide, two sets of large cells may be seen attached to the anterior end of the crop. Each set consists of seven cells, each provided with two large, internal bodies, apparently nuclei. The cells are polygonal and situated close together. By detaching the mass from the crop and floating it out in water it may be seen to be connected by a very distinct duct with the upper end of the neck of the crop, close to where it joins the œsophagus (plate xi, fig. 10, *g*). This is long enough to allow the glands to lie on the upper end of the crop. On passing the glands under a cover-glass the loosely united cells spread apart and there may be seen very clearly a ramification of the main duct passing to each one of them (plate xi, figs. 3 and 4). It hence appears that in this species these cells form a compound gland of seven cells, each cell being provided with a duct of its own, the ducts of the several cells uniting and finally forming a common duct which opens into the alimentary canal at the mouth of the neck of the crop. In other Ischnoceran genera examined, including *Eurymetopus*, *Docophorus*, and *Goniodes*, these glands are present but the cells in each are more numerous. In *Eurymetopus taurus* (plate xi, fig. 5), each gland is composed of about twenty-four cells arranged mostly in two rows, although in some specimens, at the posterior end, they are three and four rows wide, so that the gland is posteriorly expanded. Each possesses two nuclear-like bodies, (one of these may be a hollow space into which the duct opens, such spaces being present in salivary cells of insects), and they are all closely pressed together so that they assume polygonal shapes. The presence of a duct is much more difficult to determine than in *Trichodectes geomydis*, but by removing the œsophagus and crop to a drop of water on a glass slide, as before, and pushing the glands away from the crop, they may be seen to be connected with the latter by a number of fine fibers. Upon focussing down on these with the microscope, one may be seen larger than the rest, possessing a double-bordered appearance characteristic of ducts when viewed with transmitted light. It is attached to the upper end of the crop at one extremity and at the other to the anterior end of the gland, where it divides close to the latter and becomes lost in the cells. By tearing the cells apart there may be seen attached to and ramifying between them, minute, delicate processes, apparently tubules.

A third set of glands opening into the anterior part of the alimentary canal are those of the head, already described in connection with the œsophageal sclerite.

With regard to the salivary glands, then, not considering those glands of the head, the two suborders differ as follows: The Amblycera possess simply two pairs of salivary organs—a gland and reservoir on each side of the alimentary canal. These are of variable shape, since they may be simple and relatively small or very large, or they may be compound, consisting of as many as twenty separate, secreting tubules. The Ischnocera possess a pair of simple, small, only slightly variable, salivary organs on each side of the alimentary canal. These are evidently the homologs of the salivary organs of the other suborders, since their ducts unite with one another in the same manner, and since their general position is the same. In addition, they have a pair of small compound glands each element of which consists of a single cell provided with a separate ductule. The species of the Amblycera are specialized individually, those of the Ischnocera as a group.

The Malpighian Tubules.—In all cases known there are four and only four Malpighian tubules. They are simple tubes generally variously dilated near their bases. This dilatation may form a short oval enlargement of the vessels as in *Docophorus lari* (plate xi, fig. 8), or it may be long, and even occupy half the length of the tube as in *Menopon titan* (plate xi, fig. 13). These enlarged parts of the tubes are very variable in size, and according to the specimen may be present and large or entirely absent in the same species. In *Colpocephalum osborni* the basal parts of the two tubes on each side are united for a short distance (plate xi, fig 7). The vessels are generally very much convoluted and form a tangled mass of tubes about the lower part of the alimentary canal. In others, however, they are straight. In *Menopon titan* they form V-shaped tubes with the bend forward and the inner arm joining the intestines. Each tube consists of an apparently structureless investing membrane (plate xi, fig. 6), of a single layer of large granular epithelium cells within this, and finially of a thin intima lining the epithelium. The lumen is narrow and irregular since the inner ends of the cells are angular, and a convexity on one side of the lumen fits into a concavity of the epithelium on the opposite side.

III. THE RESPIRATORY SYSTEM.

The tracheæ are disposed in two main trunks, one on each side of the body, reaching from the posterior end of the abdomen into the head. Spiracles are situated laterally on the dorsal side of the abdominal segments, and in some species, as *Menopon titan,* there is a spiracle on each side of the prothorax (See Kellogg, 1896). A short branch connects each spiracle with the main longitudinal trunk of the same side. Opposite the union are given off several branches to the various organs of the body. In the head the lateral trunks end by dividing into numerous branches. No dilatation of the tracheæ occurs at any point. In *Menopon titan* a large transverse trunk connects the two lateral trunks in the fourth abdominal segment.

IV. THE NERVOUS SYSTEM.

The nervous system consists of a brain and subœsophageal ganglion in the head and a large ganglion in each of the thoracic segments. From the two head ganglia are given off branches to the mouth-parts and sense-organs. Each thoracic ganglion sends laterally a large branch to the corresponding legs. The last one gives off, in addition to these, branches that go backwards into the abdomen, supplying the organs there situated. In *Eurymetopus taurus* (plate xvi, fig. 7) the brain is large, much wider than long, and consists of two lobes united in the middle line. Each lobe expands greatly laterally. The posterior border of the brain is convex, notched in the middle line. The anterior border is very concave. The brain, therefore, presents from above the appearance of being composed of two large lateral masses connected in the middle line by a narrow commissure. From each anterior outer angle a trunk passes downward and backward to the anterior end of the subœsophageal ganglion. These form the circumœsophageal commissures, and from each a small trunk runs forward to a very large frontal ganglion situated in the median line between the anterior ends of the two cerebral lobes. The subœsophageal ganglion is larger than the brain and is situated in the lower part of the head beneath the œsophagus near the occipital margin. It is somewhat triangular in shape, with one side turned forward.

The brain and subœsophageal ganglion of *Menopon titan* (plate xvi, fig. 8) are very similar to those of *Eurymetopus taurus*. Dorsoventral longitudinal sections show that the brain is rather thick and that the lateral lobes are expanded posteriorly as well as laterally. The circumœsophageal commissures are inclined at an angle of about forty-five degrees. The frontal ganglion is smaller than in *Eurymetopus taurus* and is connected by a short trunk with the upper end of each circumœsophageal commissure. From it a branch runs forward to the labium. The subœsophageal ganglion is oval in longitudinal sections. The peripheral part of each is composed of rather large cells. Fibers pass from the lower ganglion through the commissures to the outer anterior angles of the brain, where they radiate in all directions to the peripheral cells. Transverse sections of the brain of *Menopon* sp. (plate xii, figs. 1-4, *br*), followed from before backwards, show in front the small, disunited sections which farther back (fig. 1) become enlarged in an inner and ventral direction and connected with the subœsophageal ganglion (*sg*) by two short, straight trunks. The latter ganglion is very flat in front. Back of the commissures (fig. 2) the lobes of the brain enlarge and become ovoid in sections, with the large end turned inward. The subœsophageal ganglion is still flattened and slightly constricted in the middle. Sections passing through the eyes (fig. 3) show a narrow commissure passing over the pharynx connecting the previously separated cerebral lobes which are now oval in shape. The subœsophageal ganglion is still flat but slightly enlarged laterally. Still farther back (fig. 4) the transverse commissure of the brain has increased in thickness, and the subæsophageal ganglion greatly enlarged, especially laterally.

The three thoracic ganglia are large, situated close together, and each is generally larger than the one in front. In *Eurymetopus taurus* each ganglion is hexagonal viewed dorsoventrally (plate xvi, fig. 7), with two sides transverse, one in front and the other behind. The most posterior ganglion is large and joined to the mesothoracic ganglion by its anterior side. From the lateral angles, which are a little back of the middle, large trunks are given off to the legs, and from the posterior angles larger branches, one on each side, go backwards into the abdomen. The mesothoracic ganglion is smaller than the last one, but, except that the lateral edges are more nearly equal, is very similar to it. Its anterior side joins the posterior side of the one in front, and from its lateral angles trunks arise that supply the mesothoracic legs. The prothoracic ganglion is more elongated than the others and the lateral angles are relatively farther back, but as before, the leg branches arise from them. There are no interganglionic commissures between the thoracic ganglia but the prothoracic ganglion is connected with the subœsophageal ganglion by two short, longitudinal trunks. In other forms the thoracic ganglia are a little more separated, but in all cases known, the nervous system is much concentrated and ganglia never occur in the abdomen. Longitudinal sections of *Menopon titan* (plate x, fig. 1) show that the thoracic ganglia (g_1, g_2, and g_3) are oval longitudinally and have an outer layer of large cells like those in the head. Transverse sections of *Menopon* sp. (plate xii, figs. 5–7) show that each ganglion (g_1 and g_2) is double and very large. In *Eurymetopus taurus* (plate xvi, fig. 7) each ganglion is supplied with tracheæ from a large, transverse commissure ($t\ r$) passing transversely from one main, lateral, tracheal trunk to the other. Each of these transverse trunks is applied very closely to the posterior part of the corresponding ganglion, and gives off into the latter numerous ramifying branches.

V. THE DORSAL VESSEL.

The heart was first described by Wedl in 1855. Nitzsch says nothing about it. Kramer in 1869, briefly described that of *Lipeurus jejunus*. Grosse adds little to the descriptions given by Wedl and Kramer. Wedl found that it could be studied successfully only in living animals. According to him the heart proper of *Menopon pallidum* is one-chambered and is situated in the next to the last abdominal segment just below the dorsal wall. The inner cavity is provided in front and behind with an opening. It consists of a molecular parenchymous part on each side, and a median membranous part. From the lateral, thickened part there arise ragged prolongations reminding one of the papillary muscles of the vertebrate heart, and which terminate in fine thread-like fibers attached to the median membranous walls of the heart. To the outer side of the parenchymous part are attached on each side a bundle of tense fibers, which may be termed the right and left suspensory fibers of the heart. The dorsal aorta has a swelling at its base forming a bulbus arteriosus. This has on each side a bundle of fibers, the right and left suspensory fibers of the bulbus arteriosus. Likewise at the opposite end of the heart is a swelling forming the bulbus venosus. This has two prolongations at its posterior end which appear to be inlet tubes allowing the entrance of the blood into the bulbus venosus. At the posterior end is a median row of fibers.

Kramer describes the heart of *Lipeurus jejunus* as a long narrow tube enlarged at its posterior end. Here are attached the very much reduced wing-muscles. Wedl does not mention these but very probably refers to them when he describes the "suspensory fibers". At the posterior end, according to Kramer, are four openings to admit the blood. Wedl states that the heartbeats amount to 112–120 per minute in specimens just taken from the living host, but sink to 56–52 in specimens taken from a host that has been dead a day or so.

He further describes the manner in which the different parts of the heart and aorta contract, and also gives an account of the methods he used in making his observations. Finally he states that he examined several representatives of the Philopteridæ, such as *Lipeurus variabilis*, *Goniodes colchici*, and *Docophorus atratus*, but apparently he determined merely that the heart is present in these forms.

VI. THE REPRODUCTIVE ORGANS.

The reproductive organs of both the male and the female may be divided ontogenetically into (1) parts derived from the interior of the body, including the testes or ovaries, the vasa deferentia or oviducts, and the vesicula seminalis, ejaculatory duct or vagina and spermathæca; and (2) into parts derived from the exterior of the body, including a genital cavity in both sexes, and an eversible penis with variously developed accessory chitinous parts in the male. According to Nusbaum (1882) the embryological origin of the internal organs of *Lipeurus bacillus* and *Goniocotes hologaster* is as follows: The parts arise from four fundaments. Two of these are derived from the mesoderm and give rise to the testes or ovaries and the vasa deferentia or oviducts; the others are derived from the epiblast of the ventral side of the fourth abdominal segment, and give rise to the vesicula seminalis and ductus ejaculatorius of the male or the vagina and spermathæca of the female. The second pair subsequently unite forming the unpaired organs of the adult. The latter are hence strictly external since they originate from the epiblast of the embryo. For convenience of description, however, the parts are classified better as internal and external genitalia, in which the terms *internal* and *external* are used relatively with regard to the adult structure.

1. THE MALE ORGANS.

The Internal Male Genitalia.—The testes are either six or four in number in adults, the former number being confined to the Amblycera and the latter to the Ischnocera. In the Amblycera they are variously-shaped organs lying in the lateral parts of the adominal cavity, three on each side, one in front of the other. Each opens by a short vas deferens into a common sperm duct. In the Ischnocera the testes are two in number on each side. They are generally pyriform, having the pointed ends turned away from each other and each terminated by one or two fine threads, and having the blunt ends approximated and connected by a short, narrow commissure from which the common vas deferens arises. The other internal reproductive organs of the male are essentially alike in the two suborders. The vas deferens on each side runs generally first backward from the testis and then turns forward to enter the sperm vesicle. The latter organ is usually single, but is composed of right and left lobes which in many cases are easily separated and which are sometimes normally disconnected. In all cases their lower ends open into a common ejaculatory duct. This goes to the exterior and may be either straight or variously bent. The two halves of the sperm vesicle when not entirely separated externally are essentially distinct, since each half possesses its own lumen, into which the vas deferens of the same side opens. Figure 4, then, may be taken to represent diagrammatically the typical condition of the internal male genitalia of the whole order. The figure as it is represents more exactly the Amblyceran structure, but the Ischnoceran may be produced from it by suppressing one testis on each side and drawing the other two toward each other while their distal ends are turned in opposite directions. Nusbaum states that in *Lipeurus bacillus* and in *Goniocotes hologaster*, two Ischnoceran species, the fundaments of the testes in the embryos form each three lobes, of which the posterior two develop into testes, while the anterior one atrophies. This anterior lobe, if it represents a third testis, establishes three on each side as the typical number of testes in the whole order.

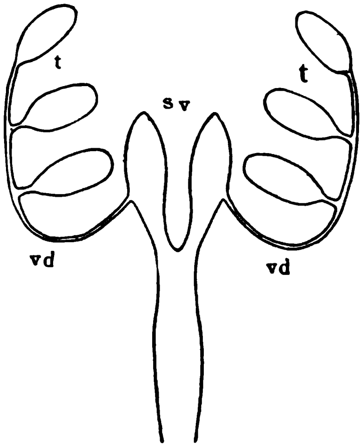


Fig. 4.—Diagram of the internal reproductive organs of the male Mallophaga; *t*, testes: *vd*, vasa deferentia; *sv*, vesicula seminalis.

In *Physostomum diffusum* (plate xiii, fig. 9) the testes are rather small. The most anterior is situated relatively rather far in front of the others, and is triangular in outline, having the base turned forward. Its posterior end becomes rather gradually narrowed, passing into the vas deferens. The middle and posterior testes are enlarged toward their bases and pointed at their distal ends. Each is connected with the vas deferens by a short vas efferens. The sperm duct runs a short distance back of the last testis and then turns forward to the seminal vesicle. This organ lies in the third abdominal segment. It is rather small, being about the length of the segment in which it is situated.

It is bilobed, being divided by median dorsal and ventral furrows into a right and left half. Each half is again partially divided by a longitudinal furrow into two secondary lobes, the outer of which is thinner than the other. From the posterior end of the vesicle a wide, almost straight ejaculatory duct passes to the exterior. Its lower half is provided with a strong, transverse musculature. The vasa deferentia appear to open into the ejaculatory duct at a point above its middle. They, however, merely become attached to this duct here, since they run forward along its sides, closely bound to it, and enter the sperm vesicle.

The vesicula seminalis of *Trinoton luridum* is elongated antero-posteriorly, tapers anteriorly, and is enlarged and rounded posteriorly. From it the ejaculatory duct runs forward and to the left. Soon it makes an abrupt bend backward and toward the middle line again, where it enters a greatly enlarged and very muscular division which opens to the exterior.

The whole reproductive system of *Menopon titan* is very greatly modified by an extreme complication of the different parts. They are all essentially the same, however, as in other species, and the modification is mostly confined to the parts developed from the exterior and to the muscles attached to these parts. These will be described farther on. The main modification of the inner organs is a great increase in the length of the ductus ejaculatorius. The testes (plate xiii, fig. 10, *t*) are oval, elongated tubes situated along the sides of the body. The most anterior on each side is connected with the anterior end of the vas deferens of the same side. The second and third are connected with the same duct at points farther back by rather long vasa efferentia. The part of the vas deferens between the first and second testes (beginning with the one in front) is longer than that between the second and third. The anterior end of each testis reaches some distance anterior to the posterior end of the one in front. Each vas deferens proceeds a short distance back of the last testis and then turns toward the median line of the body, the two are here connected by a transverse duct *(c d)* and enter the large mass of muscles surrounding the invaginated penis (this structure together with the muscles will be described under the head of the External Genitalia; see *postea*). They pass between the fibers and enter the cavity surrounded by them; turning then forward they run in this direction along the upper part of the cavity to the anterior end of the latter. Here they emerge from the muscles and go forward to the vesicula seminalis *(sv)*, each entering the side of this organ toward the set of testes with which it is in connection.

The seminal vesicle is very large, composed of two only slightly united lobes. It is elongated antero-posteriorly, tapering at both ends, and connected with the ductus ejaculatorius at its posterior ends. The latter is, as stated, a very long tube, and is consequently very much coiled. It begins at the posterior completely united end of the vesicula seminalis as a rather wide tube. It runs backwards from here only a short distance and then makes a turn toward the median line, the seminal vesicle being situated a little to the left. Here it makes a small loop upon itself and then runs forward to near the anterior end of the seminal vesicle, which reaches forward into the metathorax, making during this course a second loop upon itself. At the anterior end of the vesicula it makes a sharp bend backward, dorsal to the vesicula, and runs in a straight line to its posterior end, where it becomes narrower and turns toward the middle line. It reaches the transverse muscles of the penis and becomes here thrown into several loops, and then runs forward among the longitudinal muscles of the penis to the anterior end of the innermost (*int*) tube of the latter, with which it becomes continuous.

Nitzsch does not describe extensively the reproductive organs, merely giving a general description of them for the different suborders. He figures, however, the male organs of *Colpocephalum flavescens* and of *Menopon pallidum.* In the former (plate xiii, fig. 7) the six testes (*t*) are pear-shaped, situated with their broad ends upon the vasa deferentia (*vd*), with which they are connected by very short secondary ducts. Their pointed ends are terminated each by a short fiber. The vasa deferentia run backward and inward, uniting with the basal portion of the ductus ejaculatorius (*ej*) far from the vesicula seminalis (*sv*). The latter is somewhat elongated divided longitudinally to near its base by a median and two lateral grooves. The ejaculatory duct is very long. Immediately after leaving the vesicula seminalis it turns forward lateral of this organ and runs forward to some distance beyond its anterior end; the duct then turns backward and slightly inward, ending in a somewhat enlarged basal part to which is attached an internal chitin rod (*r*). In this form and in *Physostomum diffusum* the ductus ejaculatorius is very wide compared with this duct in *Menopon titan* and *Menopon pallidum.* In *Physostomum* it is provided with very prominent transverse muscle fibers.

In *Menopon pallidum*, as figured by Nitzsch, the testes are small, oval, and connected with the vasa deferentia by rather long ducts. The vasa deferentia are much convoluted in the portion lying between the testes and their proximal ends. The vesicula seminalis is expanded and four-lobed at its distal end, two lobes being situated on each side of the median line. From each of the two inner lobes a short twisted blind tube runs forward. The posterior end is rather pointed and passes into the ejaculatory duct. This duct is long and narrow, and is thrown into numerous convolutions, which, however, all lie between the vesicula seminalis and the external genital opening. The vasa deferentia open into the base of the ductus ejaculatorius.

The following are examples of the male organs of the Ischnocera. In *Eurymetopus taurus* (plate xiii, fig. 8) the testes (*t*) are four in number, two on each side. Each is a small pear-shaped organ having the tapering end terminated by a fine thread. The two on each side are closely connected by a rather wide commissure. They lie in the lateral part of the body cavity in the third and fourth abdominal segments close to the dorsal wall, with their long axes in an antero-posterior direction. From the inner side of the commissure connecting the testicles the vas deferens (*vd*) arises. It is a narrow tube passing first backward and inward and then forward and inward till it reaches the seminal vesicle (*sv*). Each duct enters the base of this organ on its own side. The vesicula is much the same as in *Physostomum* and *Colpocephalum*, it being partially divided into a right and left lobe by a median furrow. Each half is then again divided by median dorsal and ventral furrows on its surface. The two middle lobes of the four thus produced project farther forward than the lateral ones. Near the posterior end of the organ the four furrows cease and the ductus ejaculatorius (*ej*) takes its origin from a very short, undivided portion.

The ductus is separated from the vesicula by a constriction just in front of which the vasa deferentia terminate. The ejaculatory duct is divided into a wide, anteriorly and outwardly running, proximal part, and a narrower, longer, and posteriorly running, distal part. The two meet in front at an acute angle. The proximal dilated part is well provided with transverse circular muscles; the distal portion is also provided with muscles but not so prominently as the other. The ductus opens into the penis, but this will be described under the next heading.

The testes (*t*) of *Goniodes cervinicornis* (plate xiii, fig. 3) are rather more elongated than those of the last species described, but otherwise very similar. Their larger ends are approximated, and connected by a commissure narrower and longer than in *Eurymetopus*. The vasa deferentia (*vd*) are simple tubes passing from the commissure backwards and then forwards to the seminal vesicle (*sv*). They enter the latter, however, far up, almost at the midlateral points. In this form the vesicle is completely divided to its base into a right and a left lobe. Each lobe is elongated, tapering in front and behind. It is enlarged in its anterior half, and joined a little below its middle point by the vas deferens of the same side. The two lobes are connected with the upper end of the ductus ejaculatorius, whose lumen is formed by the union of the cavities of the seminal vesicle. A short, backward-running, proximal part of the ductus is comparatively very narrow. It soon, however, enters on the right a greatly enlarged division of the duct, which extends anteriorly and to the right of the vesicula. It is longer than the latter, wide through the middle, and narrowed at each end. Anteriorly it gradually contracts into the comparatively narrow, backward-running part of the duct. This proceeds to the penis, and in its course makes a bend to the left back of the seminal vesicle, then, after reaching the middle line of the body, goes straight to the exterior. The upper enlarged part of the duct is strongly muscular.

Nitzsch figures the male organs of two Ischnoceran species, *Goniocotes compar* and *Lipeurus jejunus*. In the former the pear-shaped testes abut closely upon each other by their large ends, and from between them the vas deferens passes by a convoluted course to the upper end of a posterior enlarged part of the ejaculatory duct. The latter is long and rather slender for most of its length. It makes a large bend forward as in the other species described, the inner arm of the loop likewise is considerably dilated, but a narrow neck intervenes between this part and the vesicula. The latter is partially divided anteriorly into two lobes.

Kramer (1869) describes very fully the male reproductive organs of *Lipeurus jejunus*. According to him the two testes on each side are acorn-shaped, having their pointed ends terminating in a fine-branched fiber. They are formed by a continuation of the outer homogeneous covering of the testes. Just where they leave the testes they contain three or four nucleated cells beyond which they become solid threads. Each divides into two main branches which are attached to the dorsal tube, but also by side branches to the Malpighian vessels and to other organs, so that they are simply members of the connective fibers that bind all the organs together. The slender vas deferens arises from the united larger ends of the testes. It consists of an outer structureless covering and an inner cellular epithelium. He describes the vesicula seminalis as an accessory secreting gland, stating that the vasa deferentia enter it and continue through it as an integral part, and then pass out as its duct forming the ductus ejaculatorius. Exception to this view will be taken farther on. According to Kramer the vesicula consists of a rather long duct and of the gland proper, the former widening itself suddenly into the latter. The walls of the duct are composed of several superimposed parts; surrounding all is a loose mass of fibers which are partly nerves and partly connective threads. Within this is a fine structureless coat only here and there provided with distinct nuclei, which is continous over the whole gland. Below this is a thick coat of cells in several layers. Lining the duct is a two-layered intima; where the duct passes into the gland the two layers diverge, the outer passing over the outside of the gland just beneath the outermost structureless membrane of the duct, which, as stated, passes over the whole gland also, and the inner continuing into the cavities of the gland as their intima. The cells of the cellular layer of the duct are contractile and appear to be muscle-cells corresponding with the muscular cells of the œsophagus and crop. At the lower end of the gland the vasa deferentia penetrate the two outer membranes and run forward beneath a series of wide cell-like plates, with which, however, they do not unite. They proceed forward thus, surrounded by the plates as by a sheath, along the middle of the flat surface of the gland to near its upper end, where they first enter its interior and then within traverse again its whole length. Within the gland they are surrounded by its secreting cells; at its lower end they unite to form the ductus ejaculatorius. It is to be noted that the muscle-cell layer of the duct continues for only a short distance over the base of the gland, the latter being situated within the cells as a flower in its calyx. Kramer further describes the penis and its muscles, and also the origin of the sperm and formation of the spermatophores.

Transverse sections through the testes of *Menopon titan* show that each is surrounded by a structureless outer tunica. Within this is an epithelium of high narrow cells projecting irregularly with ragged edges into the lumen of the organ. They are all more or less curved and together present somewhat the appearance of an iris diaphragm (plate xiii, fig. 1). An intima is apparently absent. The lumen of the testes is not very large and is filled, in prepared specimens, with a granular substance which is probably a coagulated fluid. The vasa deferentia have an outer tunica resembling that of the testes, within this a single-layered cellular epithelium. The cells are much smaller and relatively a great deal shorter than those of the testes (plate xiii, fig. 2). The lumen is small and lined by a thin structureless intima covering the inner ends of the epithelium cells. The seminal vesicle is composed of the same elements as the vasa deferentia. The epithelium cells are columnar but comparatively short (plate xiii, figs. 5 and 6). The lumen on the other hand is very large and filled with an apparently coagulated (in mounted specimens) non-cellular substance. The organ in sections is clearly seen to be a double structure, for the two halves are almost entirely separate. The two cavities communicate only through the upper end of the ejaculatory duct. The main connection between the two lobes is by an apparently outer layer of the tunica, which in the groove between the two sides passes across from one to the other, and an inner layer continuing around its respective lobe. In some places, however, in the basal half of the organ, the inner layers of the tunicas are absent and the opposing cells fused. The ejaculatory duct (plate xiii, fig. 4) has the same structure as the seminal vesicle and vasa deferentia. Outside of its tunica, however, is a layer of circular muscle fibers. These continue a short distance over the base of the seminal vesicle (plate xiii, fig. 5) and unite the lower ends of its lobes more firmly, but they soon cease.

From the preceding descriptions it is evident that figure 4, on page 177, represents the typical development of the internal genital organs of the males for the whole order. The only constant difference between the two orders in respect to these organs is the number and relative position of the testes. The latter organs have no constant form in the Amblycera although the variation is small, while on the other hand, in the Ischnocera the form is almost entirely constant. Thus, with respect to the sperm glands, as was found to be the case also with the salivary glands, the Ischnocera are specialized as a group, while the Amblycera are specialized among themselves on a less evolved type.

It now remains to consider the nature of the structure referred to as the vesicula seminalis. As stated, Kramer regarded it as an accessory gland, but he did not show what its function as a gland is. He found, further, that the spermatophores are not formed in the male ducts, but in the female spermathæca. That it is composed of united right and left organs is very evident. This is indicated by the fact that it is actually entirely divided into two lateral lobes in at least one form, and in others it is more or less deeply cleft, while in none known is it without a median groove. Further, according to Nusbaum (1882), it actually arises from two separated fundaments in the embryo, which subsequently unite. Kramer states that since the secreting cells are arranged around two tubes, the vasa deferentia, the organ has the appearance of being composed of two closely united glands, and that a separating wall is actually present. Grosse (1885) disagrees with Kramer and regards the structure as consisting of two bladder-like enlargements of the ductus ejaculatorius, which serve to retain the spermatozoa as they come from the testes until sent to the exterior by the contraction of the vesicle. According to him, accumulations of spermatozoa are to be found in the upper part of the organ. He states also that a secreting power cannot be denied to the cells forming the wall. The walls are thick and have a glandular appearance, but, other than this, proof of their secreting function appears to be absent.

The embryological investigations of Nusbaum, if correct, show clearly the relation of the vesicula seminalis to the adjacent parts. As has been shown, the vesicula generally presents a four-lobed appearance, being divided by three longitudinal constrictions of which the median one is the most constant and the best marked. According to Nusbaum the vasa deferentia unite with the fundaments of the reproductive organs derived from the epiblast. The latter then become each produced into two lobes at their anterior ends before they fuse with each other. Then, when they unite, there is produced a structure having a four-lobed anterior end to which the vasa deferentia are attached, and an undivided posterior part. The former becomes the vesicula seminalis and the latter by elongation the ductus ejaculatorius.

The External Male Genitalia.—The outer accessory structures connected with the inner reproductive organs have never been very carefully studied. Nitzsch (1818), Piaget (1880, 1885), and Taschenberg (1882) described them mostly as they appeared through the body-wall. Piaget made a few dissections. The external organs consist of two parts: (1) a simple or compound invagination of the body-wall of the last abdominal segment, and (2) chitinous parts developed in the walls of the invagination. In addition, however, there are muscles attached to these parts, situated within the body, and which are very important and sometimes very complicated adjuncts of the copulatory organs. The following descriptions represent all the genera of which males could be obtained.

Eurymetopus taurus (Plate XIV, fig. 5, plate XV, fig. 1).

The male has nine abdominal segments. The last tergum is very much narrowed from side to side, forming a triangular terminal dorsal plate with the apex, which is a little invaginated, projecting backwards. The sternum of the last segment, on the other hand, is much enlarged, projecting much beyond the corresponding tergum both posteriorly and laterally as a large plate with slightly upcurved lateral edges. Above this plate the top of the copulatory organ may be seen projecting a little beyond the end of the tergum. By separating these two plates a terminal cavity of the abdomen is exposed, having the chitinous penis lying along the middle line of its floor, and the anus opening into the upper posterior part. This space will be spoken of as the *genital cavity*, since it is evidently formed to accommodate the reproductive function, and since it contains the external part of the copulatory organ. The opening of the alimentary canal into it is apparently a secondary result, since the anus is terminal and exposed in the female when the genital cavity is in front of the last sternum.

Longitudinal sections through the male show that the genital cavity is formed by a wide invagination of the hind end of the abdomen (plate xv, fig. 1). The cavity is almost as wide as the body itself, and extends from the posterior border of the last segment far into the eighth. In its upper wall near the posterior margin is the anal opening (*a*). From its inner end an evagination of much smaller diameter than the primary invagination takes place, forming a long, rather slender, distally tapering tube in whose walls a thick deposit of chitin is present. This is the penis (*p*). From its base a large, wide chitinous plate extends forward *within* the body-cavity (*pl*). The part of the penis lying within the genital cavity will be spoken of as the *external* part of the penis, and the plate extending forward within the body cavity as the *internal* part. It is to be noted, however, that the plate is strictly external, since it is simply a part of the chitinous covering of the body, and that it is internal only in the sense that an inward-running process of the body-wall is internal. The genital chamber reaches much farther forward below the penis than above it. At the point where the internal and external parts of the penis are continuous, the ductus ejaculatorius (*ej*) enters into the evagination of which the outer part is formed, and opens by a terminal orifice to the exterior. The internal plate extends forward beneath the ductus ejaculatorius and close to the ventral wall of the body to the anterior border of the second abdominal segment. To it the muscles (*em*) of the penis are attached.

The penis (plate xiv, fig. 5) as a whole is a dorsoventrally flattened structure. Its anterior three-fourths is wide, forming the internal plate, while the posterior one-fourth is wide at its base but rapidly tapers beyond this. The posterior fourth is the external part formed by the chitinous thickening of the evagination described. Where the two meet, a large, square area is taken out of the penis. The margins at the side of and behind this are very thick. From the former arise two wide processes, one on each side, which rapidly contract and curve dorsally and inwards, almost meeting each other in the middle line. In front of these, two other processes arise from the anterior margin of the non-chitinized space, as two backward prolongations from the inner edges of the thickened lateral margins of the plate in front. They extend backward, outward, and slightly ventrally, terminating beyond the posterior edges of the lateral processes, and almost reaching across the unchitinized space. They are narrower than the lateral processes and taper but slightly. From the posterior thickened margin of the unchitinized area a third pair of processes arises. These are short, rapidly tapering, and continuous with the ventral edge of the transverse part behind the unchitinized area, this part being, as before stated, tubular. These processes lie close together, each just to one side of the median line. Their inner edges are slightly divergent and their outer edges strongly convergent and concave. Their tips reach about as far forward as the posterior ends of the processes in front. There are thus six processes—two in front, two behind, and one on each side—arching over the unchitinized space of the chitinous penis. They surround the terminal portion of the ejaculatory duct, since the latter passes beneath the arch formed by the dorsal processes on its way to the external tubular part of the penis. The several processes serve, however, partly for the attachment of muscles. The anterior half of the internal plate is comparatively very thin and tapers to a blunt termination in front. Back of the middle, also, the plate contracts somewhat toward its base. The external penis has a large, thick, basal part, which rapidly contracts to a slender, tubular, distal part, terminating by an arrowhead-shaped enlargement, the posterior angles of which are very sharp. This terminal tube curves downward a little toward its tip (plate xv, fig. 1), where its inner cavity opens to the exterior.

To the anterior end of the chitinous penis on its ventral side are attached two wide sets of muscle fibers. These pass backward, outward, and a little ventrally to the ventral wall of the abdomen. Each set is parallel-sided and arises from the penis just to one side of the middle line, and as the two diverge backwards they form only a very small angle with each other. To the other end of the penis are attached four sets of muscles, two dorsal and one on each side. Each lateral bundle is attached to one side of the enlarged subterminal part of the penis. It passes forward and outward, forming an angle of about 45° with the penis, to the lateral wall of the body-cavity. The dorsal muscles are near the middle line, and extend anteriorly, outward, and dorsally. These posterior sets are shorter than the anterior ones, ending on the body walls in the fourth and fifth segments.

The mechanism of the chitinous parts, invaginated tube, and muscles is self-apparent. The anterior muscles contracting push the chitinous penis backward, and it carries outward the partly evaginated inner tube of the genital cavity, the flexible walls of which become erected. In this way the external part of the penis can be protruded from the genital cavity, which during the operation becomes itself more or less erected. The posterior sets of muscles contracting reverse these movements, resulting in a withdrawal of the penis into the genital chamber.

Docophorus lari (Plate XIV, fig. 8).

The chitinous genitalia in this species consist of a large, thin, flat chitinous plate situated within the abdomen close to the ventral wall, and an external, conical tube with two articulated lateral arms. The plate is rather short, being less than twice as long as wide. Its greatest breadth is near its posterior end; it tapers somewhat forward but has a wide rounded anterior termination. The external part is tubular and represents an inner tube evaginated from the anterior end of the genital cavity. Its walls are very thick and entirely chitinous. In general shape it is, as stated, conical, having the internal plate passing forward from the ventral part of the anterior end. Its lateral outlines are slightly convex. Posteriorly it terminates in a slender median prolongation, at the extremity of which is the external genital opening. Into the anterior end of this part, dorsal to the internal plate, the ductus ejaculatorius enters. Five processes surround the slender, parallel-sided terminal tube. Two of them are dorsal, two lateral—one on each side, and one ventral. The latter is triangular in shape, rather elongated antero-posteriorly, and has the more pointed apex pointed backwards in the median line. The dorsal processes are much longer than the ventral one. Each is a flat plate reaching almost to the posterior end of the central tube. It expands toward its middle and then tapers off again beyond this point. The approximated edges are straight and lie each just to one side of the middle line, while the outer edges are very angularly convex. The lateral processes are short and thick, somewhat hook-shaped, with the ends turned outward. They reach a little beyond the ventral plate.

Two long curved rods are attached externally to the lateral aspects of the base of the outer part of the penis. Their anterior ends, by which they are movably articulated, are considerably enlarged. Each is curved throughout its length, so that the outer margin is convex and the tips, which extend a little farther backward than the median parts, converge. The part of the penis between these processes is very strongly chitinous. The lateral margins of the internal plate are much more strongly chitinized than the median part, so that in a cleared and mounted specimen the former alone show through the body wall. Consequently there is the appearance of an internal pair of rods extending forward from the bases of the external pair; and in many of the figures of Nitzsch, Piaget, and Taschenberg the chitinous genitalia of the males are represented as if this were the case. The plates serve, as in *Eurymetopus taurus*, for the attachment of muscles. One specimen was found with the penis protruded. The lateral external rods were turned forward, over the back of the insect, so that the median conical part was left projecting backward and upward alone. It is not very clear what the function of the rods is, since there are numerous forms, as will be shown, in which they are absent. The turned-forward position is probably not abnormal, since they were found thus in several specimens of other species, and some of the drawings of Piaget show them the same. They have the appearance of acting as a guard to the penis, or they may also serve as levers to prevent the latter from being pushed back into the genital cavity. The penis, however, is otherwise very much the same as in those forms where movable rods are absent.

Nirmus pacificus.

The penis is very similar to that of *Docophorus lari.* The internal part is a wide plate which tapers slightly forward and ends anteriorly with a wide rounded outline. The proximal half of each lateral margin is slightly convex and very thickly chitinized, so that the two give the appearance of a pair of curved prongs reaching forward into the body cavity, since the median part of the plate is comparatively very thin and transparent. Between the internal plate and the outer parts is a thickened portion common to both. The external penis consists of two lateral curved rods articulated to the base of the median external part. When the penis is retracted within the genital chamber, these two rods extend backward with their tips approximated and their concave edges turned toward each other. When, however, the penis is protruded, the rods turn forward over the back of the insect and become rotated outwards, so that their convex edges are toward each other and their tips divergent. The median external part is prolonged terminally into a slender, tapering, chitinous tube, which appears to bear at its end the genital opening. Surrounding this are five processes which arise near its base and are much the same as those of *Docophorus lari.* On the dorsal side is a pair of rather long slender plates, on the ventral side a slender median rod, and on each side a rather large, outward-turned process reaching a little beyond the extremity of the ventral rod. Ventrad of these last are two small cusps. The dorsal laminæ are much longer than the others, but the central tube projects a little beyond them. The last abdominal sternum is a wide, rounded plate which projects backwards so as to lie beneath the penis when this organ is protruded.

Giebelia mirabilis. (Plate XIV, fig. 4).

In this species the penis consists of the same parts as the two last described, there being present an internal plate, an external conical median part, and two lateral processes. The plate is wide and comparatively very short, its length being only a little greater than its breadth. It lies within the body close to the ventral wall, and to its dorsal surface muscles are attached. The sides are a little concave, its anterior border straight with corners rounded. The lateral basal parts are thicker than the rest. The external intromittent part of the penis is short, wide, with convex lateral edges, rapidly contracting distally, and ending in the middle line with a short, narrower prolongation. This is not entirely chitinized as in the other forms described for its distal half is almost membranous. At the base of the internal plate on its dorsal side the ductus ejaculatorius enters the external penis. The two lateral processes are short and thick, each being only a little longer than half the internal plate. They are curved, having the convex edges turned outward. They converge posteriorly but the tips are turned straight backwards forming an angle with the rest, so that the terminal parts lie parallel with each other. Their bases are enlarged and movably articulated to the rest of the penis as in the other forms described. The articulation is the same as that between the segments of the body and the joints of the legs; i. e., the parts are continuous but non-chitinized where the articulation occurs.

Goniodes cervinicornis. (Plate XIV, fig. 2).

The penis can be protruded for a distance about equal to three segments of the abdomen. The outer part consists of a delicate membranous tube evaginated from the inner end of the genital chamber. It is protected by three chitinous processes arising from a circular chitinization surrounding the base of the membranous penis. Two of the processes are lateral, long, slender, tapering, and somewhat convergent, with the outer edges convex and the inner concave. The third is ventral and median. It is a narrow chitinous rod having the distal end triangularly expanded, terminating some distance in front of the posterior ends of the lateral processes. These parts are free from the wall of the membranous penis but closely surround it. Lying within the dorsal wall of the latter is a thin, wide, chitinous plate arising also from the circular chitinous base of the penis. It is shorter than the ventral process, and has its edges a little concave. From the anterior ventral margin of the basal part of the external penis a large, thin, parallel-sided, chitinous plate, having a rounded anterior edge and slightly concave lateral edges, arises and passes forward within the body-cavity, giving attachment to protrusor and retractor muscles. It lies close to the ventral wall of the body-cavity, and at its base the ejaculatory duct enters the external penis. The opening into the latter is overhung by a wide tapering plate. The membranous penis extends beyond the ends of all the chitinous parts. When the chitinous structure is pushed outwards the outer processes and the common chitinous base are entirely exposed. It is to be noted that in this species the lateral processes of the external penis are not, as in *Docophorus*, *Nirmus*, and *Giebelia*, movably articulated to the base, and also that the median part is much less extensively chitinized.

Lipeurus fuliginosus major. (Plate XIV, fig. 1).

In this species the chitinous genital parts form a fork-shaped structure. A long, narrow plate lies within the body, representing the handle, while the external part consists of two prongs. The internal plate is comparatively much narrower than in any of the species so far described. It is a little contracted from side to side toward its base. Distally it gradually tapers to a blunt termination. Its posterior end expands suddenly and becomes bifid. Each arm is very short and extends backwards and outward, forming an angle of about 45° with the plate. The posterior borders of the two form a concavely rounded edge to their end of the plate. Attached to the posterior end of each of these prongs is a lengthened knife-like piece which extends backwards into the genital cavity. The two are dissimilar. The one on the left is larger, being both longer and wider, but they differ in still other respects. The left one has its outer edge convex proximally and concave distally; the inner edge of the same shows similar curves but in opposite order. The end tapers down to a point directed somewhat outwards. The outer edge of the right smaller prong has an outline corresponding with that of the inner edge of the left prong. That is, it is concave toward its base and convex toward its tip. The inner edge is convex at the middle, decidedly concave proximally and slightly so distally. Hence its point is turned inward—relatively opposite to that of the left prong.

The bifid posterior end of the internal plate is imbedded in the base of the chitinous penis. The outer prongs are attached to the arms of the bifurcation in a manner much different from that in other forms. The base of each prong is a little expanded and bears two tapering processes projecting inwardly and anteriorly, one lying dorsal to the other. The dorsal process is the larger; it is curved so that the posterior margin is concave and the anterior convex. The tips of the dorsal processes of the two sides are directed toward and lie close to each other. Each is connected by a delicate dorsoventrally flattened chitinous bar, which passes outward to the arm on the same side of the bifid base of the internal plate, and fuses with it very near its posterior ends. The ventral process is smaller than the dorsal one; its posterior edge is convex and its anterior edge concave. The end of each arm of the plate abuts upon the corresponding prong between the bases of the two processes of the latter, the transverse slender bar of chitin serving to connect the two otherwise separated parts. Lying in the dorsal wall of the membranous penis is a thin chitinous plate. It extends from near the bases of the lateral prongs to a short distance from the distal end of the smaller one. It also is symmetrical. The right edge is about straight and distinctly marked; it lies nearer the side of the penis than does the left edge, so that the plate is not median. The left edge is much less sharply defined and extends obliquely from the left side of the base of the penis posteriorly and toward the middle line. To the dorsal side of the internal plate is attached a large mass of muscle fibers, and on the same side of the plate the ductus ejaculatorius enters the penis.

Oncophorus bisetosus californicus.

There is nothing in the genitalia of this form different from those already described. The chitinous parts consist of a rather wide internal plate with thickened margins and transparent central part, and of an outer median tapering chitinous intromittent organ with articulated lateral processes. Piaget figures *Oncophorus unguiculatus* in which the genitalia are apparently the same as in the form just described.

Goniocotes creber. (Plate XIV, fig. 9).

In this form the chitinous genitalia are extremely reduced. Within the body is a long narrow plate reaching almost to the anterior end of the abdomen. It is very thin and transparent except laterally, where it is weakly chitinized, giving the appearance of two long, very delicate, slightly curved rods lying within the body. Each of these is continuous externally in the wall of the penis. Their outer parts are more chitinized, the tips sharp and convergent. Muscles are attached to the internal part. Piaget figures several species of *Goniocotes* in which the chitinous genital parts are about the same as in *G. creber*, consisting of an internal plate with external prongs. In some the plate is evidently more chitinized than in this form.

The species whose genitalia have been described are all Ischnoceran forms; the following belong to the Amblycera and it will be seen that the genitalia are more simple than in the others, though essentially the same.

Trinoton luridum. (Plate XIV, fig. 7).

A genital chamber is present with a membranous penis arising from its inner end. The chitinous parts consist of a long, slender, tapering rod running forward within the body cavity from the base of the penis. Its posterior end is expanded and bifid, the prongs being external and imbedded in the wall of the penis. They extend posteriorly and a little outwards, each being a little longer than half the length of the internal rod. Each prong ends bluntly posteriorly, but some distance in front of its posterior end it gives off a process wide at its base but soon narrowing very much, which runs dorsally a short distance and then turns posteriorly, extending in this direction parallel with the main prong from which it arises past the posterior end of the latter, and then turns inward to meet and fuse with the corresponding process of the other side. This median part is very weakly chitinized. The arc thus formed lies in the dorsal wall of the membranous penis, while the two prongs are lateral. The penis extends some distance beyond all the chitinous parts. The ductus ejaculatorius enters it above the internal rod, which latter serves for the attachment of muscles. The intromittent organ in this form, then, consists of a membranous tube evaginated from the inner end of the genital chamber, in whose walls chitinous rods are developed which unite anteriorly to the ventral wall of the tube and send forward a chitinous rod into the body cavity.

Colpocephalum osborni. (Plate XIV, fig. 6).

The genitalia of this species are very similar to those of *Trinoton luridum* just described. The only difference is that the processes arising from near the posterior ends of the prongs of the fork-shaped structure do not meet each other. In addition to these, however, there is present in the dorsal wall of the membranous penis a chitinous arrowhead-shaped plate, which reaches about half way to the ends of the lateral prongs and is connected with the latter by wings from its base, which reach the prongs a short distance back of their divergence. There are also developed in the walls of the penis numerous small, granular chitinizations.

Physostomum diffusum. (Plate XIV, fig. 3).

The chitinous genital parts of this species are very simple. There are present in the walls of the penis two diverging lateral rods which meet in front. Here they send forward into the body cavity a very small rod, it being about a third of the length of each outer prong, to which muscle fibers are attached. The posterior ends of the prongs are connected by a transverse, angular bar.

Menopon mesoleucum. (Plate XIV, fig. 10).

A long, rather thick internal rod is present. This arises from the united anterior ends of two thick bars in the walls of the penis. These bars are very short and do not nearly reach the end of the penis. To the end of each is articulated a longer tapering rod free from the penis and reaching to its posterior end. These have the appearance of being homologs of the articulated lateral prongs in some of the Ischnoceran forms.

RÉSUMÉ.

From the preceding descriptions it is clear that the outer genitalia of the male may be generalized as follows. The posterior end of the last abdominal segment is invaginated to a varying extent, forming a genital chamber surrounded by the walls of the body, possessing a chitinous lining continuous with the body-wall, and opening posteriorly to the exterior. Into its anterior end the ductus ejaculatorius opens, and the part in which the operation occurs is carried backward as an invagination forming an internal tube arising from the anterior wall of the genital chamber. This tube is the penis. Figure 5 represents diagrammatically what has just been described. It is evident that if the inner walls of the genital chamber are flexible the penis could be entirely protruded from the cavity containing it. Specimens killed in alcohol are often found with the penis projecting in this manner. The anal segment is lacking, so that the rectum opens into the genital chamber.

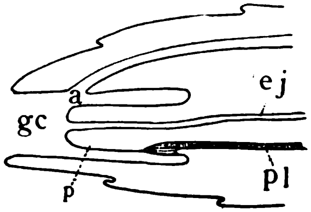
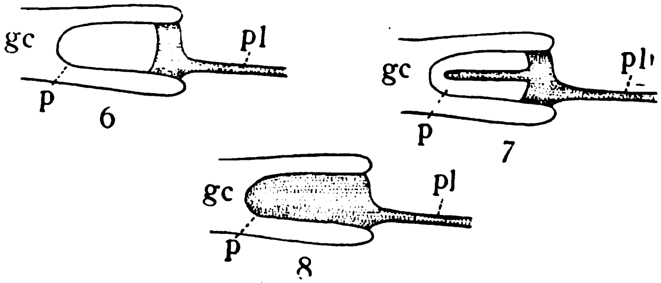


Fig. 5.—Diagram of external genitalia of male Mallophaga; *a*, anus; *gc*, genital chamber; *ej*, ejaculatory duct; *p*, penis; *pl*, internal plate arising from chitinous thickening in base of penis.

The chitinous genitalia are formed as chitinizations in the walls of the inner tube. The object of this is double, (1) to strengthen the walls of the penis, (2) to give attachment to muscles for protruding and retracting the penis. The latter function is apparently the more important, since a contrivance for its accommodation is never absent, while chitinous parts strengthening the penis are in some cases very slightly developed and in a few, such as in *Menopon titan*, yet to be described, and in some species of *Colpocephalum*, are entirely absent. The structure which gives attachment to the muscles is always of the form of a chitinous prolongation into the body cavity from a chitinization in the ventral part of the base of the penis. It may, therefore, be represented as in figure 5, *pl*. This internal structure may be short or long and either narrow or broad, but it is always essentially the same and lies ventral to the ductus ejaculatorius. The external parts are developed as various degrees of chitinization radiating through the walls of the penis from the ventral basal chitinous deposit. The simplest and most usual form consists of a rod given off backward on each side (fig. 6) such as in *Menopon mesoleucum*, *Trinoton luridum*, *Colpocephalum osborni*, and others.



Figs. 6–8.—Diagram showing successive degrees of chitinization in walls of penis; *p*, penis; *gc*, genital chambers; *pl*, internal plate.

Secondary processes may be developed from these. In others the basal chitin may completely surround the penis (fig. 7) and, besides lateral processes, may give off dorsal and ventral ones as in *Goniodes cervinicornis*. Further, this circular basal chitinization may extend continuously backward (fig. 8) and transform the penis into a chitinous tube, as in *Docophorus lari* and in *Eurymetopus taurus*. Independent chitinizations may also be developed in the penis, taking the form of plates and granulations in its walls, as in *Lipeurus fuliginosus major*. It cannot be stated whether the articulated lateral processes are homologous with the non-articulated lateral pieces or not—embryology must decide this. However, since the two are not known to be present in the same form, and since in *Goniodes cervinicornis*, at least there are non-articulated processes free from the lateral walls of the penis, it might be inferred that the two may be homologous.

Comparison shows that the simplest forms of external genitalia occur in the Amblycera, and that in none of these are the parts much complicated. On the other hand, the genitalia in nearly all the Ischnocera are very much more developed, and are characterized by a much wider spreading of the chitin in the walls of the penis, and of a relatively much larger development of the internal process. The condition of the external reproductive organs in the two suborders hence agrees with that of the internal organs, for it was before shown that the latter are the more specialized in the Ischnocera.

The structure of the intromittent apparatus of *Menopon titan* will now be described (plate xiii, fig. 10, and plate xv, figs. 2–5). It is so very highly developed and so complicated, being much more so than in any other form known, that it is more easily understood after a study of the more typical structure found in other species. Grosse has described it but apparently not very correctly. He says that the last abdominal segment of the male is invaginated and runs forward in the body to the border of the last and penultimate segments, and then goes again backwards in order to continue anew anteriorly, tube-like, to the sixth segment. Surrounding this are transverse muscles, and attached to its anterior end longitudinal muscles. He next states that within the invaginated segment is a tube open at both ends, which anteriorly passes into a gradually decreasing chitinous rod reaching to the third abdominal segment, and that within this tube is still another which continues anteriorly into a whip-lash beset with numerous spines or bristles. It is rather hard to imagine how structures such as these could exist in the manner described; and dissected specimens, entire specimens cleared with *Eau de Labarraque* and stained, and sections cut in longitudinal and transverse directions, indicate that Grosse's description is not entirely correct. The structure of the various parts which Grosse has mentioned is apparently as described in the following account.

When the abdomen of the male is opened from above there is to be seen in it, lying along the middle line and ventral to the alimentary canal, a large, compact mass of muscles reaching from the last segment into the fourth. The posterior three-fourths of this mass is composed of transverse fibers, and the anterior one-fourth of longitudinal fibers which converge to a point in the fourth segment. This structure forms the most prominent organ in the abdomen and is easily taken entire from the body by detaching it from the body-wall at the posterior end. Under a low-power lens it can easily be seen that the transverse muscles of the posterior three-fourths are much curved, but are a little less than semicircular. Their dorsal ends are attached to a vertical sheet of membrane which extends down between them from above as a fold from a thin membrane surrounding the whole mass. Their lower ends are attached to a thin, transverse, ventral plate. By dissecting the fibers apart it is found that they, together with the ventral plate to which their lower ends are attached, surround a cylindrical cavity. Within this is a thin-walled, membranous tube open in front. This latter contains a second thicker and more chitinous tube and a chitin rod. The rod arises posteriorly from the inner tube. Between the outer tube and the muscles on the dorsal side of the former lie the forward-running parts of the vasa deferentia. These enter the muscles posteriorly and then pass into the upper part of the cavity within them, run forward to the anterior end of this, and then emerge to join soon the seminal vesicle. The inner tube and rod pass forward some distance beyond the anterior end of the outer tube, and the former is thrown into several convolutions which vary in different specimens. The anterior longitudinal muscles arise from the anterior end of the mass of transverse muscles and converge upon the tip of the chitin rod. From these a small band of fibers continues into the thorax, where it is attached to the floor of the metathorax in the middle line. The transverse muscles, when detached from the ventral plate, but left with their upper ends still joined to the vertical membrane, have very much the appearance of a bunch of fire-crackers, the fold of membrane representing the axial fuse.

The inner tube on account of its being more strongly chitinous than the other appears dark, while the outer is transparent. The interior of the inner tube is beset with numerous chitinous projections. In the posterior part these are of the form of small conical processes closely distributed over the walls. Somewhat farther forward they increase in length and form sharp backward-pointing teeth. Still farther in front they become much more elongated, and anterior to these they take the form of large backward-projecting, spike-shaped appendages having sharp points, and they almost obstruct the lumen of the tube. Beyond these a decrease in size of the processes takes place, and in the walls of the anterior part of the tube they are entirely lacking, the tube being here transparent. Beginning at the posterior end the tube runs straight forward to near the anterior end of the transverse muscles. In the longitudinal muscles it becomes folded and a loop may project from the latter. It is here of greatest diameter. It becomes narrowed in the part that has no internal processes and gradually passes into the comparatively narrow ejaculatory duct. To its posterior end the chitin rod is attached. This is circular in transverse sections, rather long since it reaches into the fourth segment, and tapering anteriorly. It is curved, having the convexity to the right and dorsally.

The relationships of these different parts is very clearly shown by transverse and longitudinal sections (plate xv, figs. 2–5). The posterior end of the last (the ninth) abdominal segment is deeply invaginated, the invagination running forward into the fifth segment. The walls of the tube thus formed (plate xv, figs. 2, 3, 4, t_1) are very thin and transparent, being entirely non-chitinized. In the anterior part of the sixth segment, however, they begin to increase in thickness and continue to become thicker from here forward to their anterior ends in the fifth segment. Here they turn away from the axis of the tube they form and then curve backwards a short distance. Then they become thin again and turn sharply forward and inward, closely following the inner face of the first bend. This is the beginning of an evagination which extends backwards almost to the beginning of the first. The walls of this are likewise very thin and transparent, and are closely applied, except posteriorly, to the inner surface of the first tube. There is thus formed a double-walled tube open in front and having a recurved anterior edge.

This is the outer of the two tubular structures to be observed by dissection alone and it is surrounded by the transverse muscle-fibers (plate xv, figs. 2, 3, 4, t_1 and t_2). This is probably what Grosse referred to as a tube open at both ends.

In the anterior part of the eighth segment the walls of the inner tube diverge from those of the outer one, leaving a free space between them connected with the exterior. A short distance back of where the two diverge the walls of the inner tube are bent backward and then again forward, forming a free cylindrical fold projecting backward. This extends posteriorly to the middle of the last segment and then ends by being invaginated and forming within itself a third tube (plate xv, figs. 2, 3, 4, t_3). The posterior part of the walls of these two are fused for a short distance and closely united as far forward as the fold in the second. Here the innermost tube becomes entirely free and lies as within a sheath surrounded by the first and second tubes. This is the inner tube so easily determined by dissection; it runs forward as before described, passing out of the cavity between the other tubes and entering the longitudinal muscles (plate xv, figs. 2 and 5 t_3, and plate xiii, fig. 10 *int*). The chitinous rod (plate xv, figs. 2-5, *r*, and plate xiii, fig. 10, *r*) is attached to the fused part of the second and third tubes back of the posterior fold of the former. Only its anterior end is shown in median longitudinal sections. It is the homolog of the internal rods or plates of the chitinous genitalia already described.

It is readily seen that the intromittent organ of *Menopon titan* is simply an exaggeration of the type of that found in other species. It consists first of a deep invagination of the body-wall, extending from the posterior end of the last abdominal segment forward into the fifth. (Grosse states that this is the turned-in tenth segment of the male. Beyond the fact that the male has one segment less in the abdomen than the female, he gives no evidence for this conclusion). The cavity thus formed corresponds exactly with the genital chamber of other species. Into the posterior part of it the rectum opens from above. Its anterior end is evaginated, and the tube thus formed is homologous with the membranous penis of other forms. It is almost destitute of chitinization, however; the rod arising in other species from the base of the penis is here situated near the tip. It appears from this that the elongation of the parts has been brought about, not by a deepening of the genital cavity with a corresponding lengthening of the penis in a posterior direction, but by a deepening of the genital cavity with a lengthening of the penis in front of its base. The innermost tube is produced by an invagination of the posterior end of the penis and is either unrepresented in other forms or is comparatively extremely short. Figure 9 represents diagrammatically the relation of the several tubes, and a comparison of this figure with fig. 5 shows the similarity of structure. (cf. also plate xv, fig. 2 with fig. 1).

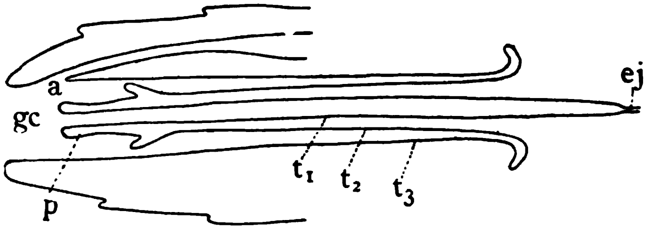


Fig. 9.—Diagram of Intromittent organ of *Menopon titan*, male; *a*, anus; *gc*, genital chamber; *ej*, ejaculatory duct; *p*, penis; t_1, innermost invaginated tube; t_2, middle invaginated tube; t_3, outermost invaginated tube or wall of genital chamber (cf. fig. 5).

The muscles surrounding the tubular structures are also very complex, as has been shown. The plate to which the ventral ends of the transverse fibers are attached arises from the body-wall between the sterna of the eighth and ninth segments of the abdomen (plate xv, figs. 2 and 4, *p*). The proximal end of this plate is non-chitinized but farther forward it becomes darker. It ends in the ventral part of the groove formed by the recurved ends of the first and second tubes. Its lateral edges curve somewhat dorsally. The muscles are surrounded by a very thin, delicate membrane (plate xv, fig. 2, *m*) which along the median dorsal line sends a fold downward a short distance to which the upper ends of the transverse muscles are attached. In the middle the muscles are seven or eight fibers deep but the number lessens toward each end. They curve laterally around the tubes and each layer is attached to the ventral plate internal to the layer just outside it.

The longitudinal muscles, as stated, form a conical mass of fibers converging upon the anterior end of the rod, from which a few run forward to the sternum of the metathorax. There are a few transverse muscles within the others, especially close around the contained tube (plate xv, figs. 2 and 5, *lm*). It is rather difficult to determine how the longitudinal muscles are attached posteriorly. It appears clear, however, that they are not attached to any of the tubes but to the ventral plate, and in the following manner: The anterior end of the plate curves laterally very much upward around the outermost tube. The upper lateral and dorsal fibers posteriorly, in front of the recurved anterior ends of the first and second tubes, curve downward and inward, crossing each other in the middle line. They then turn backward, passing over the rim of the tubes, and are attached mostly to the lateral ventral aspects of the anterior end of the ventral plate, but a few are attached on the dorsal side. The lower lateral and ventral muscles likewise cross each other in the middle line in front of the tubes and are attached to the lateral aspects of the dorsal side of the anterior end of the ventral plate. The mechanism of this complex structure is rather hard to understand. It is evident that the contraction of the longitudinal muscles must push the rod outwards, carrying with it the innermost tube. The posterior fold in the second tube appears also, as if present to accommodate such an action. Grosse states that during copulation the whole inner tube is everted. It is difficult to understand what it is for if it is not made use of in this way, but it is much more difficult to see by what means it is turned out, since in front of the attachment of the rod at its posterior end it is entirely free from everything except the ejaculatory duct. Those specimens examined in which the inner tube was most everted had this protruded only as far as the base of the rod, the longest length apparently possible, judging from the structure of the parts. There can be little doubt that the band of muscles connecting the anterior end of the rod with the floor of the metathorax serves to draw the rod back. The transverse muscles may serve to prevent the lateral bending of the rod while the longitudinal muscles are contracting.

2. THE FEMALE ORGANS.

The reproductive organs of the female consist, like those of the male, of internal and external parts. The external part consists merely of the genital cavity, with the abdominal sternum forming its floor produced into a variously modified plate. The genital cavity differs from that of the male in not being situated in the terminal segment of the body, but by being found as an invagination of the ventral body-wall several segments forward. It also does not contain the anal opening, this being situated terminally in the last segment.

The external parts of the female are much the same in all forms and the female *Menopon titan* may be described as a type of the whole order. Grosse describes the female organs of this form, but only very briefly, and he says nothing at all of the external parts. The sternum of the eighth abdominal segment is considerably modified. It consists mostly of a large depressed plate (plate xvii, fig. 7, *pl*) produced on each side into two ventrally projecting ridges divergent behind. The posterior border is free, above it is the external genital opening *(gc)*, a narrow transversely elongated aperture. It opens into a cavity, the genital chamber, situated above the plate. The structure is best studied by means of transverse and longitudinal sections. Longitudinal sections (plate xvii, fig. 6) show that the genital chamber *(gc)* is formed as an invagination of the sternum of the eighth abdominal segment, a short distance in front of the posterior border of the latter. The vagina *(v)* opens into the upper part of its anterior end by a terminal downward curvature. It is lined by a continuation of the chitinous wall of the body. Transverse sections (plate xvii, figs. 1-3) show that the depressed plate of the eighth abdominal sternum is W-shaped. The tergum of the segment forms a large, continuous, arched plate extending on each side to the lateral edge of the body. Here a non-chitinized line occurs, separating the tergum from a pleural chitinization situated laterally on the ventral aspect. The inner edges of these are united by unchitinized spaces with the outer arms of the W-shaped sternum. Each angle of this, again, is free from chitin. The lateral walls are thick and especially so at their bases, where they are produced into a large, inward-projecting ridge *(b)*. The non-chitinization of the angles of the sternum and of its union with the pleural sclerites makes it evident that it is formed to enlarge by a diverging of the sides of the lower angles when an egg passes into the genital chamber. The inner lining *(ci)* of the latter is thin but mostly chitinized. A large mass of transverse muscles *(tm)* surround the inner wall, being attached latterly to the walls of the sternum and their enlarged bases. Back of the vaginal opening their inner ends are attached to a longitudinal dorsal crest of the inner wall of the cavity. A few longitudinal muscles *(lm)* also are present.

The genital cavity is wide posteriorly but becomes narrower in front. It is almost divided into two longitudinal chambers by the dorsal ridge of the ventral groove of the sternum. The vagina opens into its anterior end somewhat to the right. This is a large tube and must be regarded as a part of the exterior since it possesses a chitinous intima continuous through that of the genital cavity with the exterior covering of the body. From the genital chamber the vagina (plate xvii, figs. 2–5, *vo*, *av*, *pv*, and *cv*) runs a short distance dorsally and then turns forward. It forms a large U-shaped tube (plate xvi, fig. 3, *va*) lying in the ventral part of the abdominal cavity, with the closed end reaching far forward. Sometimes it is somewhat spirally twisted upon itself. The anteriorly running arm begins at the anterior end of the genital cavity to the right of the other backward running arm (plate xvii, figs. 2, 3, 4, *vo*, *av*, *pv*). The latter is generally expanded near its middle but becomes narrower posteriorly, reaching back of the opening of the other arm into the genital chamber. Here it makes a bend to the right (plate xvii, fig. 1, *pv*) and becomes continuous with the oviduct (*od*).

The muscles surrounding the genital cavity are continuous over the vagina, forming circular muscles around it which continue throughout its whole length. Outside of these are a few transverse muscles. Grosse states that the muscles begin near the opening. Within the muscles is a structureless membrane which forms the true outer covering of the vagina. Within this is a cellular epithelium lined by a chitinous intima thrown into large folds projecting into the lumen.

The oviduct (plate xvii, figs. 1–6, *od*) is very long and somewhat coiled. It varies greatly in different specimens, but always runs forward from the anterior end of the vagina as an apparent continuation of it. It is first closely or openly bent upon itself, and then runs again forward to near the anterior end of the vagina, where it bifurcates, each tube running outward and backward, bearing at its end the egg-tubes of the same side. According to the specimen the oviduct may be very narrow or greatly distended. It is formed of the same elements as the vagina except that it lacks the chitinous intima. The inner ends of the epithelium cells (plate xvi, fig. 4, *ep*) project irregularly into the lumen, and the latter is generally almost obliterated by the approximation of the cells, which are much larger than those of the vagina. The muscle layers, on the other hand, are not so thick.

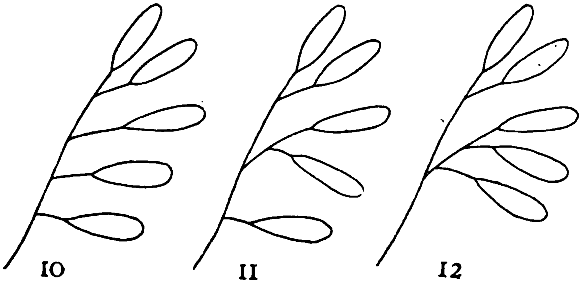
The egg-tubes are five in number on each side. They arise from the distal ends of the oviducts and have the same structure that they show except that the outer covering of muscles is lacking. Each is a long slender tube dilated where it contains ova into chambers which decrease in size distally. The five tubes on each side are united at their anterior ends and form a tangled mass on each side of the body. Each tube (plate xvi, fig. 6) is surrounded by a close, outer, structureless membrana propria (*mp*). Within this is an epithelium composed of a single layer of cells. When there is no egg present in the ovary these cells are all very large (plate xvii, figs. 3–5, *o*) and almost fill the lumen of each tube. They appear triangular in transverse sections, while their bases on the membrana propria are polygonal. A large, radially elongated nucleus is present in each. When ova are present in the ovaries the egg-tubes present a very different appearance (plate xvi, fig. 6). Each egg is surrounded by a follicle formed by an enlargement of the tubule. In the lower chambers (*a*) are to be found fully formed eggs (*o*). They are surrounded by a thick egg-covering filled with granular yolk. In form they are elongated and flattened at each end. The epithelium (*ep*) of the walls of a lowermost egg-chamber is composed mostly of small cubical cells. Posteriorly they are elongated, forming a transverse posterior wall for the chamber in the middle of which is the opening into the proximal part of the tubule connecting the egg-chambers with the oviduct. In front the epithelial cells become successively longer, until the most anterior are very long and slender, those from opposite sides almost meeting one another. In front of these are four immensely enlarged cells (*ac*) entirely filling the lumen of the tubule and thus closing the anterior end of the egg-chamber. These retain the form of the cells of an inactive tubule. The small epithelial cells are lined by a distinct intima, which is apparently absent when there is no egg present and the cells are large.

The smaller egg-chambers (*b*) contain a granular mass of yolk (*g*) which is not surrounded by a covering of its own. The epithelium is the same as in the lower chamber, except that the anterior cells are not elongated. Filling the anterior end of the enlargement of the tubule are six large cells. The part of the tubules connecting two egg-chambers is slender, with small epithelial cells.

Grosse states that there is present on each side of the vagina a club-shaped spermathæca. In the specimens of *Menopon titan* examined, however, there was no organ of this kind present.

In *Eurymetopus taurus* (plate xvi, fig. 1) the vagina *(va)* consists of a large, wide, straight, invaginated tube reaching forward to the fifth abdominal segment. Into its anterior end open two oviducts, one from each side. Into the posterior end on the dorsal side a duct opens, connected at its distal end with a large, dorsoventrally flattened, glandular organ *(g)*. The cells of this are very large and distinct (plate xvi, fig. 2). The duct is divided into a wide distal and narrower proximal part. The posterior end of the first is invaginated and the second part arises from the inner end of this. Numerous muscle-fibers *(m)* are attached to the upper part around its middle. Spermatozoa were not found in the gland. This appendage is constant, but the pouch referred to varies a great deal.

The oviducts are simple tubes extending outward, anteriorly and dorsally into the fourth segment. They are sometimes narrow tubes with enlarged bases and are sometimes wide throughout their whole length. Each bears at its distal end five egg-tubules. These sometimes join the oviduct serially as in fig. 10, or two or more may be united at their bases as shown in figs. 11 and 12.



Figs. 10–12.—Variations in attachment of egg-tubules to the oviduct in *Eurymetopus taurus.*

Nitzsch states that in the Ischnocera there are five egg-tubes present in the females, while in the Amblycera there are but three. He expresses a doubt though whether this second statement holds for the suborder. Rudow (1870) states that in both groups five are present but that in the Amblycera (*Liotheum*) two remain rudimentary. Even this statement is not entirely true, for there are five well developed in the adult *Menopon titan.* Sections of a young *Menopon persignatum* show four fully formed tubules and one small one. Adults of *Colpocephalum osborni* show three well developed and one small one on each side. In *Trinoton luridum* there are four in the adult. Grosse in his paper on the anatomy of *Tetrophthalmus chilensis* (*Menopon titan*) quotes Nitzsch's statements in regard to the number of egg-tubes, but adds no observations on the number present in the form he describes. Nitzsch figures the female organs of *Menopon mesoleucum.* According to him there is present a short, wide vagina, narrowed in front where it gives off on each side an oviduct. Each of these bears distally three egg-tubes. A double spermathæca opens into the base of the vagina. He figures also *Goniodes dissimilis*, in which the vagina is a straight tube branching in front into two rather wide oviducts into which open five egg-tubes. Into the posterior side of each duct three blind tubes open internal to the ovarian tubules. Kramer describes the female organs of *Lipeurus jejunus*, giving five as the number of egg-tubes present.

From the descriptions just given it is evident that the two suborders differ from each other in regard to the female organs simply in that there is a tendency amongst Amblyceran forms toward a reduction of the number of ovarian tubules from five—the constant number in the Ischnocera—to three.

The eggs (plate xvii, fig. 8) are large, oval, and generally rather elongated. They are attached to the bases of the feathers singly or in groups. On birds badly infested large numbers of eggs may be found. They are fastened by one end, having that end from which the embryo will emerge directed toward the tip of the feather. When the embryo leaves the egg it pushes off a circular cap and partly protrudes itself. In *Docophorus fuliginosus* the embryos apparently remain in the mouth of the open egg for some time, for many were found in this position. Some found thus were very immature (plate xvii, figs. 9 and 10), having the mandibles entirely unchitinized, the maxillæ almost as large as the mandibles, and the labium large, consisting of a transverse basal position and two lateral lobes. The most immature of those found free from the egg had the mandibles well chitinized.

Little has been done on the embryology of the Mallophaga. The work of Nusbaum (1882) on the development of the reproductive organs has already been referred to. Melnikow (1869) made a more general study of the embryology, but since he concluded from his investigations that the Mallophaga are closely related to the Pediculidæ—a conclusion entirely untenable—his work cannot be very accurate. He proves that there is present a beak but no labium, and hence that the mouth-parts are Hemipteran!

VII. SUMMARY.

The foregoing descriptions of the various systems of organs of the Mallophaga show that the two suborders are separated by wide structural differences. These may be tabulated as follows:

Amblycera.	*Ischnocera.*
Mesonotum and Metanotum Distinct.	**Mesonotum and Metanotum Fused.**
Antennæ concealed.	Antennæ exposed.
Antennæ clavate.	Antennæ not clavate.
Mandibles horizontal.	Mandibles vertical.
Labial palpi present.	Labial palpi absent.
Paraglossæ various in form.	Paraglossæ constant in form.
Œsophageal sclerite and connected glands absent or modified.	Œsophageal sclerite and connected glands present and normal except in a few scattered cases.
Crop simple.	Crop an œsophageal diverticulum.
Salivary glands various in form.	Salivary glands constant in form.
Ingluvial glands absent.	Ingluvial glands present.
Testes six.	Testes four.
Chitinous ♂ genitalia simple.	Chitinous ♂ genitalia more complex.
Egg-tubes three to five.	Egg-tubes five.

The above table shows that in nearly every character in which the two suborders differ the Ischnocera have a more specialized organization. That the separation of the two groups is very great is shown by the fact that nearly all the important organs are affected, the heart, tracheal system, and nervous system being the only ones alike in both. The exact systematic position of the Mallophaga cannot at present be determined, since enough of the anatomy of nearly related forms is not known. Packard (1887), however, has shown that they may be closely related to the Psocidæ, and Kellogg (1896) has given further evidence of this. But if the Psocidæ are the most closely associated with the Mallophaga, in what manner the two groups are related is impossible to say. Until this is known the relationship of the two suborders of the Mallophaga to each other cannot be determined nor that of the families composing these suborders.

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EXPLANATION OF PLATES.

PLATE X.—Fig. 1, Median dorsoventral longitudinal section of anterior half of *Menopon titan; h* head, t_1 prothorax, t_2 mesothorax, t_3 metathorax; a_1 first abdominal segment, a_2 second abdominal segment, *bw* outer body-wall, *bm* basement membrane, *m* mouth-opening, *bc* buccal cavity, *p* pharynx, *œ* œsophagus, *cr* crop, *v* anterior end of ventriculus, *sg* salivary gland, *b* brain, *s.œ. g* subœsophageal ganglion, g_1 prothoracic ganglion, g_2 mesothoracic ganglion, g_3 metathoracic ganglion, *tr* trachea, *lm* longitudinal muscle, *tm* transverse muscle, *o* anterior end of an egg-tube cut near the surface. Fig. 2, Throat skeleton with attached glands of *Eurymetopus taurus; œ. s* œsophageal sclerite, *l. g* glands, *d* duct, *ch. ped* chitinous pedicle. Fig. 3, Left maxilla, ventral aspect, of *Goniodes cervinicornis*. Fig. 4, Labial fork of *Ancistrona gigas*. Fig. 5, Mandibles, ventral aspect, of *Ancistrona gigas*. Fig. 6, Mandibles, posterior aspect, of *Goniodes cervinicornis*. Fig. 7, Œsophageal sclerite, dorsal aspect, of *Eurymetopus taurus; d* duct, *do* opening of duct, *m* median groove, *ant. p.* anterior process, *c. œ* circumœsophageal process. Fig. 8, Hypopharynx of *Ancistrona gigas*. Fig. 9, Labium of *Nitzschia dubius; sm* submentum, *m* mentum, *pf* palpifer, *lp* labial palpus, *g* glossa, *pg* paraglossa. Fig. 10, Right maxilla, ventral aspect, of a *Læmobothrium*. Fig. 11, Mandibles, ventral aspect, of *Læmobothrium* sp.; *c* condyles, *r* right mandible, *l* left mandible. Fig. 12, Right mandible, posterior aspect, of *Goniodes cervinicornis; c* condyle, *ch pls* chitinous plates. Fig. 13, Labium, ventral aspect, of *Eurymetopus taurus; sm* submentum, *m* mentum, *g* glossa, *pg* paraglossa.

PLATE XI.—Fig. 1, Salivary glands of *Trichodectes geomydis; a* outer gland, *b* inner gland. Fig. 2, Salivary organs of *Menopon titan* (after Grosse); *a* salivary gland, *b* saliva reservoir. Fig. 3, Large-celled salivary gland of *Trichodectes geomydis*, with the cells in natural position; *d* duct. Fig. 4, Same as last but with cells spread apart showing branches of duct (*d*) to individual cells. Fig. 5, Large-celled gland of *Eurymetopus taurus; d* duct. Fig. 6, Longitudinal section of part of Malpighian tubule of *Menopon titan; mp* membrana propria, *ep* epithelium, *in* intima. Fig. 7, Part of alimentary canal with Malpighian tubules of *Colpocephalum osborni; v* lower end of ventriculus, *i* upper end of intestine. Fig. 8, Alimentary canal of *Docophorus lari*. Fig. 9, Crop (*cr*) with part of œsophagus and ventriculus of a *Trichodectes* from a horse. Fig. 10, Alimentary canal of *Trichodectes geomydis; g* large-celled glands of crop. Fig. 11, Alimentary canal of *Eurymetopus taurus*, ventral view; *r* outer salivary gland or saliva reservoir, g_1 inner gland, g_2 large-celled gland. Fig. 12, Alimentary canal of *Goniodes cervinicornis*. Fig. 13, Alimentary canal of *Menopon titan*.

PLATE XII.—Transverse sections of *Menopon persignatum*. Fig. 1, Section through head in region of anterior end of brain. Fig. 2, Section through head in region of posterior part of antennary fossæ. Fig. 3, Section through head, passing through the eyes. Fig. 4, Section through posterior part of head. Fig. 5, Section through prothorax just back of the legs. Fig. 6, Section of mesothorax through bases of the legs. Fig. 7, Section of metathorax just in front of the legs; *œ* œsophagus, *an* antenna, *br* brain, *sg* subœsophageal ganglion, *e* eye, *tr* trachea, *h* heart, *l* base of mesothoracic leg, *f* fat-body, *cr* crop, g_1 prothoracic ganglion, g_2 mesothoracic ganglion, *c* nerve commissure in front of mesothoracic ganglion, *vw* thickened ventral wall of antennary fossa.

PLATE XIII.—Internal male genitalia. Fig. 1, Transverse section of testis of *Menopon titan; mp* outer tunica, *ep* epithelium. Fig. 2, Transverse section of vas deferens of *Menopon titan; mp* membrana propria, *ep* epithelium, *in* intima. Fig. 3, Reproductive organs of male *Goniodes cervinicornis; t* testes, *vd* vas deferens, *sv* vesiculæ seminales, *ej* ductus ejaculatorius. Fig. 4, Transverse section of ductus ejaculatorius of *Menopon titan; mp* membrana propria, *ep* epithelium, *in* intima, *m* circular muscles. Fig. 5, Transverse section of lower end of vesicula seminalis of *Menopon titan;* letters as in last. Fig. 6, Transverse section through middle of vesicula seminalis of *Menopon titan;* letters as in fig. 4. Fig. 7, Reproductive organs of male *Colpocephalum flavescens* (after Nitzsch); *t* testes, *vd* vas deferens, *sv* seminal vesicle, *ej* ductus ejaculatorius, *r* chitinous rod attached to inner tube of genital cavity. Fig. 8, Same of *Eurymetopus taurus;* letters as before. Fig. 9, Same of *Physostomum diffusum;* letters as before. Fig. 10, Same of *Menopon titan;* letters as before, but also, *ve* vas deferens, *cd* transverse duct connecting the two vasa deferentia, *int* innermost invaginated tube of genital cavity, having rod (*r*) attached to its lower end.

PLATE XIV.—External male genitalia. Fig. 1, Chitinous genital parts of *Lipeurus fuliginosus major*, dorsal aspect. Fig. 2, Same of *Goniodes cervinicornis*, dorsal aspect. Fig. 3, Same of *Physostomum diffusum*. Fig. 4, Same of *Giebelia mirabilis*. Fig. 5, Same of *Eurymetopus taurus*, dorsal aspect. Fig. 6, Same of *Colpocephalum osborni*. Fig. 7, Same of *Trinoton luridum*. Fig. 8, Same of *Docophorus lari*. Fig. 9, Same of *Goniocotes creber*. Fig. 10, Same of *Menopon mesoleucum*.

PLATE XV.—Fig. 1, Longitudinal section of two posterior somites of male *Eurymetopus taurus*. Fig. 2, Longitudinal section of six posterior segments of male *Menopon titan*. Figs. 3–5, Transverse sections of abdomen of male *Menopon titan*. Fig. 3, Through anterior end of segment VIII. Fig. 4, Through segment VII. Fig. 5, Through segment V; *tm* transverse muscles; *lm* longitudinal muscles, *em* extrusor muscles, *m* membrane surrounding muscles, *gc* genital chamber, *i* intestine, *a* anus, *p* penis, *pl* internal plate, *r* internal rod, t_1 outermost invaginated tube,

t_2 middle tube, t_3 innermost tube, *re* anterior recurved edges of outer and middle tubes, *t* testes, *vd* vas deferens, *sv* seminal vesicle, *ej* ejaculatory duct, *vp* ventral plate to which transverse muscles are attached, *mt* Malpighian tubule, *f* fat-body, *tr* trachea, *tg* tergum, *s* sternum, *p* pleuron.

PLATE XVI.—Fig. 1, Reproductive organs of female *Eurymetopus taurus*; *o* ovaries, *od* oviduct, *va* vagina, *sp* spermathæca, *g* gland. Fig. 2, Accessory gland of female *Eurymetopus taurus*; *d* duct, *m* attached muscles. Fig. 3, Reproductive organs of female *Menopon titan*; *o* ovaries, *od* oviduct, *va* vagina. Fig. 4, Transverse section of oviduct of *Menopon titan*; *ep* epithelium, *m* circular muscles, *mp* membrana propria. Fig. 5, Detached egg-cap (See plate xvii, fig. 8). Fig. 6, Longitudinal section through an egg-tube of *Menopon titan; a* lowermost egg-chamber containing a mature egg (*o*), *b* an upper egg-chamber containing an immature egg (*g*), *ep* small epithelial cells forming side-walls of egg-chambers, *ac* very large epithelial cells filling the anterior ends of egg-chambers, *mp* membrana propria, *in* intima, *od* oviduct. Fig. 7, Nervous system of *Eurymetopus taurus*; *b* brain, *sg* subœsophageal ganglion, g_1 prothoracic ganglion, g_2 mesothoracic ganglion, g_3 metathoracic ganglion, *tr* trachea. Fig. 8, Longitudinal dorsoventral section of brain (*b*) and subœsophageal ganglion (*sg*), passing through the circumœsophageal commissure of *Menopon titan*; *fg* frontal ganglion.

PLATE XVII.—Figs. 1–5, Transverse sections through posterior end of abdomen of female *Menopon titan*, from behind forward: Fig. 1, through middle of genital cavity (*gc*); Fig. 2, through the beginning of the vagina (*vo*); Fig. 3, cut in front of vaginal opening; Fig. 4, taken in front of genital cavity; Fig. 5, through anterior end of vagina; *r* rectum, *rg* rectal glands, *tr* trachea, *f* fat-body, *gc* genital cavity, *tm* transverse muscles, *lm* longitudinal muscles, *ci* inner chitinous wall of genital chamber, *b* enlarged base of outer chitinous wall of genital chamber, *vo* vaginal opening into anterior part of genital chamber, *av* anteriorly running part of vagina, *pv* posteriorly running part of vagina, *cv* anterior end of vagina where the two arms meet, *o* egg-tubes, *pr* prerectal part of intestine, *od* sections through the coils of the oviduct. Fig. 6, Longitudinal dorsoventral section of five posterior abdominal segments of female *Menopon titan; bw* chitin wall of body, *bm* basement membrane, *m* longitudinal muscles, *a* anus, *r* rectum, *rtm* transverse muscles of rectum, *ch* chitinous lining of rectum, *rg* rectal glands, *gc* genital chamber, *v* vagina, *vtm* transverse muscles of vagina, *od* sections of oviduct. Fig. 7, Ventral view of posterior end of abdomen of female of *Menopon titan;* VII, VIII, IX, X segments of abdomen, *pl* plate forming ventral wall of genital cavity, *gc* opening of genital cavity to exterior. Fig. 8, Three eggs attached to shaft of a feather; *a* egg containing an embryo, *b* empty egg with cap off. Figs. 9 and 10, Young nymphs just hatched; *lb* labrum, *mn* mandible, mx_1 maxilla, mx_2 labium, *an* antenna, *m* mouth-opening.

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CONTRIBUTIONS TO BIOLOGY
FROM
THE HOPKINS SEASIDE LABORATORY
OF THE
LELAND STANFORD JR. UNIVERSITY

XX

The Nature of the Association of Alga and Fungus in Lichens.

BY

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PREFATORY NOTE.

This memoir is the twentieth of a series designed to illustrate investigations and explorations connected with the Hopkins Seaside Laboratory, an adjunct of the biological laboratories of the Leland Stanford Junior University. These investigations have been carried on by means of the assistance given by Timothy Hopkins, Esq., of Menlo Park, California. This memoir appears in the publications of the California Academy of Sciences, the present edition being a reprint.

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Directors Hopkins Laboratory.

Date of publication, June 5, 1899.

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I. INTRODUCTION.

THE last few years have seen a revival of interest, gratifyingly widespread, in the study of lichens. Except during the few years immediately following the writings of DeBary, Schwendener and Reinke, which wrought a revolution in our conception of lichens, they have been studied mainly by systematists. These found in macroscopic characters all that was required to determine an old or to describe a new species. Every one must have felt, even before Reinke recently recalled the question so forcibly to the minds of botanists, that by no means the last word had been said about these interesting organisms, and that the study of

May 13, 1899.

other than superficial characters would repay the investigator. To the physiologist they especially appeal because they are not simple organisms, but an association of two simple organisms.

The nature of the association is variously regarded, from pure parasitism of one member upon the other, to association mutually beneficial, if not absolutely necessary, to the two. Schwendener has always regarded the association as pure parasitism of the fungus upon the alga, and his school advocates the same view. The opposite view is held by Reinke (1894) and his sympathizers, of whom Schneider (1896*a*) is at the moment perhaps the most conspicuous in this country. Reinke believes that the association is what he names Consortism, and that the "Consortium" is as "autonomous" as any plant.

A question to which there are such opposite answers by such eminent investigators cannot be regarded as answered at all. This paper is a contribution to the discussion, and I shall be glad if the account of my work and its results leads at all to the solution of the problem. I must remark at the outset that much of my work may not be new; how much I cannot say, for though I have tried, I have not been able to have access to all the literature on this subject. Furthermore, no one should venture, from the study of only a few forms, to draw conclusions regarding a great number, although the careful examination of a few forms will justify opinions regarding the others, if only these opinions are held tentatively, subject to modification by further researches.

Beginning with *Ramalina reticulata* Krplhbr., a lichen so large that it forms a conspicuous feature of the landscape in some parts of California, I have examined several species and genera of lichens occurring hereabouts, and not trusting merely to microtome sections of "fixed" material, I have had recourse to experiments and cultures on and of living material. The difficulty of minutely studying lichens alive is notoriously great, not least because of their extremely slow growth. Yet in their rates of growth there must be great diversity. I am inclined to believe that *Ramalina reticulata* grows more rapidly than most. My reasons are based on the universal occurrence of large specimens all about here, and also upon the behavior of this lichen in cultures. As emphasized by Benecke (1898) in a recent paper on the culture of Algæ, and earlier by Möller (1887), the difficulty of excluding bacteria from cultures made from vegetating, and even from spore, material, is very great. The presence of bacteria in a culture will at least delay and obscure, if it does not vitiate, the results; and yet to exclude the bacteria is impossible with our present crude culture-technique. The almost invariably gelatinous nature of the exterior of the lichen body renders the removal of the bacteria from the surface impossible. During the latter part of a long dry season, the surface of such a lichen as *Ramalina reticulata* must be so dry, at least by day, that it is not likely to hold the bacteria or the fungus-spores that fall upon it, though they may easily remain caught in some angle or slight irregularity. During and for some time after a rain, in a fog or on a dewy night, on the other hand, the gelatinous surface will be moist, at least sufficiently so in spots to cause whatever bacteria and fungus-spores fall upon it to stick. Möller (1887) recommends washing as thoroughly as possible in clean running water, the aim being to remove by the stream, as well as by floating, whatever may have fallen upon the surface. By this means he partially cleansed the apothecia from which he intended to collect spores for his cultures.

Defective as such cleansing is for the apothecia, which are not especially gelatinous on the surface, it is still more so for the much more gelatinous surface of the thallus. The running water does remove some of the foreign objects, but some of the most gelatinous of these (for example, bacteria in the vegetative condition) cling to the gelatinous surface of the thallus in spite of the most thorough attempts to dislodge them. For this reason, even if sterilized water be used for the washing, a discouragingly large proportion of the thallus fragments used for culture are accompanied by bacteria which multiply only too rapidly. In spite of thorough sterilization of the slides, cover-glasses, vessels and instruments used in connection with the cultures, and the utmost pains to prevent the introduction into the cultures of organisms from outside, I have failed in most cases to make pure cultures, because the lichen fragments themselves carried bacteria, and substances nutritious for them, into the culture-media. In many cases, however, the number of bacteria was constantly small.

For most of my cultures I used the "hanging-drop" method of the bacteriologist, employing for the purpose slides with two concavities, ground sufficiently deep to avoid contact of the drop with the bottom of the concavity. The cover-glasses were sealed upon the slide with vaseline. If the concavities are reasonably large and deep (e. g. 13 mm. diameter, 1 mm. depth) a hanging-drop surrounded by an adequate volume of air, and large enough to supply food-material for several weeks, may be used. It must be admitted, however, that hanging-drop cultures have only a limited usefulness, for the food-supply presently becomes exhausted, and there may accumulate in the drop undue amounts of the dissolved excreta of the organisms present.

Various methods have been employed by others in preparing material for culture. As culture-media for the spores and lichen fragments, I have experimented with boiled tap-water, with the moisture carried by the spores expelled upon the cover-glass, with a drop of the ordinary nutrient beef-gelatine of the bacteriologist, with similar nutrient agar-agar, and with the distilled water used for general purposes in the laboratory. The distilled water was poisonous. I did not consider it necessary to determine the reason for this, though one would suspect it of being acid and possibly of containing traces of copper or other injurious salts. The distilled water prepared in quantity in the chemical laboratory, and supplied by it to the other laboratories of this University, is sufficiently pure for ordinary purposes, but it is ill-suited to culture experiments on living organisms, as repeated experience shows. The effect of our distilled water on motile bacteria is marked and immediate. Bacteria actively motile in the media in which they are cultivated in the laboratory will continue to be motile at the same rate if placed in a drop of sterilized tap-water. Transferred either from the culture directly or from sterilized tap-water into which they have been inoculated, to a drop of distilled water, they promptly come to rest and will not recover their motility. The unsatisfactoriness of our distilled water for lichen cultures may, therefore, be attributed to some poison in it and not to the lack of oxygen, for boiled tap-water will be at least as free from oxygen as ordinary distilled water.

The nutrient agar-agar and gelatine above mentioned were made with tap-water (not distilled water) and had previously been proved to be well adapted to bacteria culture. In the lichen cultures also they were perfectly wholesome, as attested by the only too rapid growth of whatever bacteria were carried into the drops by the spores.

II. THE GERMINATION OF SPORES.

The generally practiced method of obtaining lichen-spores for cover-glass cultures is the following:—the thoroughly cleansed and sterilized cover-glasses, either dry or with a drop of some sterilized nutrient medium, are so placed that some of the spores discharged from an apothecium will strike upon them. The lichen material was prepared thus: fresh specimens of *R. reticulata*, brought into the laboratory from the trees on which they were growing, were brushed and shaken to remove loose dust, etc., from the surface, cut into small pieces, each piece having only one apothecium, and placed on moistened filter-paper in a Petri dish and covered. Near each apothecium, but not touching the lichen, was placed a cover-glass prepared as just described, and supported in such an inclined position that bacteria, etc., which might be floating in the air in the

Petri dish could not settle on the surface intended for the culture. The sterilized cover-glasses, although carefully kept "butter-side down," might readily become infected by air-currents set up by the necessary movement of the cover-glass and by lowering the cover of the Petri dish. Apart from such accidental infection, the possibility of which was carefully reduced to the minimum, the only bacteria which could get into the cultures were those carried in with the spores. The considerable force with which the spores are discharged is indicated, as others have repeatedly shown, by the distance to which they go. This force is developed by the swelling, when wet, of the gelatinous walls of the paraphyses and other cells forming the contents and the walls of the apothecia. In less than five hours, enough spores will usually be ejaculated upon the cover-glass to justify sealing it over a concave slide.

Spores collected thus upon cover-glasses spread thin with agar-agar or gelatine germinated in seven days. At the same time I collected spores upon cover-glasses introduced dry into the Petri dish. Owing to the cooling of the laboratory (from morning, when I set cover-glasses to collect spores, to afternoon, when I sealed the cover-glasses on the concave slides) there accumulated on the cover-glasses not only the moisture carried by the spores, but also that condensed from the damp air in the dish. Thus a supply of water at least adequate for germination was insured, whatever may be said of the nutrient value of such water. After the same lapse of time (seven days) spores had germinated on these cover-glasses.

In all the cultures the number of spores germinated was very small in proportion to the number sown. If I had sufficient confidence in the suitableness of agar-agar and gelatine for lichen cultures, and in the nutritive value of the condensed and spore-carried water, I might draw a definite and significant conclusion regarding the value of the spores of *R. reticulata* as reproductive bodies. I do not feel justified in doing this, though I will call attention to two things. First, there must be a very considerable number of spores discharged, both in nature and in the laboratory, before they are ripe and whenever the apothecia are wet. Second, that by bearing this in mind and by using trustworthy culture media for such cover-glass preparations, subjecting them to otherwise normal conditions of warmth, light and aëration, the percentage of ripe spores capable of germination could be determined. From these data the relative values of the spore-method and the purely vegetative method of dispersal could be ascertained. This is, however, hardly necessary, for, as I have shown in a previous paper (1898), the great majority of the specimens of *R. reticulata* to be found about here are evidently fragments, while only very few have grown where they are from the spore. This lichen may, earlier in its history, have produced even more spores in each apothecium and more apothecia than now, but this would seem hardly necessary, considering the ease with which fruiting specimens and an abundance of spores may be obtained at all seasons. It seems more probable that in this lichen, as is claimed also for others, superiority of the purely vegetative method of dissemination (by means of fragments torn away by the wind) is resulting in the decrease of the germinating power of the spores.

The superiority of the vegetative method of reproduction is two-fold: it insures the presence in the new place of both members of the lichen association—the hyphæ and the gonidia, as is the case in the soredia of other lichens—and it results in much wider dispersal than is possible with spores or soredia. The vegetative method of dissemination of this lichen, so evidently a very valuable one and perhaps the most perfect among lichens, may well react on the production of spores; if not already as to their number, then certainly as to their quality.

Although the spores germinated in the same length of time and in about the same numbers (proportionally) in the agar-agar, gelatine and water cultures, the subsequent development was unequal. In three days after the first germinations were observed, the germ-tubes had grown somewhat but had not branched in the agar-agar and very few if any more spores had germinated, whereas in the water culture the tubes were longer, some of them had branched, as fig. 3 shows, and the number of spores germinated had increased considerably. In eight days more, that is, in eighteen days after the spores were collected on the cover-glasses, growth had ceased in all the cultures. The differences between the water cultures on the one hand, and the agar and gelatine cultures on the other, were now still more evident. The germinated and ungerminated spores in the water cultures still looked healthy, and the number of bacteria in the cultures was comparatively small. In the other cultures, however, there were many spores evidently dead, the remainder looked unhealthy, the germinated ones least so, and the number of bacteria flourishing on and in the agar-agar and the gelatine was sufficiently large to justify the inference that they were an important if not the sole cause of the unsatisfactory condition of the spores.

The contents of the spores which appeared to be alive at all were far less highly refractive than at first; perhaps, but not wholly, because of the consumption of the oil which was stored in them in the form of drops of very considerable size (figs. 1 *a* and *b*, 2, 3 and 4). The death of the spores was marked by certain changes in the cell contents: the protoplasm lost its granular character and gradually became indistinguishable from the wall and the cell-sap, the oil drops spread, became confluent with one another, later appeared to fill the whole cavity of the cell, and finally disappeared altogether, leaving only the empty cell-wall. Minutely to follow the disorganization-phenomena ("Disorganizationserscheinungen") is very difficult, owing to the small size of these two-celled spores.

From what I have noticed, I can only suspect, not conclude, that the spores were killed and disorganized by the products of the discouragingly active bacteria. That the same appearances may be produced in another way is shown by a water culture made as above described, but with the hollow below the cover-glass filled with sterilized tap-water. In this preparation the spores all died within three days, the protoplasm disappeared, the oil drops became confluent and filled the cell-cavities. Excess of water, inadequate diffusion of oxygen and carbon-dioxide, checked respiration, the diffusion into the water of some poison contained in the vaseline used for sealing — all or any of these may have been the cause of death and of the breaking down of the cell-contents. Bacteria were practically absent.

If it were possible to clean an apothecium so thoroughly that no bacteria would be carried by the spores ejected upon the cover-glass, it seems probable that agar-agar would prove a good medium upon which to cultivate lichens from the spores. This is conceivable but not readily attainable. If practicable, agar-agar cover-glass cultures would be very useful, for they could be minutely watched with the high powers of the microscope.

In the cultures just described, made during the latter part of the rainy season, in February, only one cell in each spore put out a germ-tube. Water cultures begun about the middle of March, when it was warmer out of doors and the rains were practically over, were more successful in that both cells of some spores germinated, though in all of these the tubes from the two cells were unequal in length, and only one tube from a spore branched.

Having obtained germinated spores by means of these cultures, I attempted to reconstruct a *Ramalina* by putting these where they could easily reach gonidia from a *Ramalina* thallus. The method employed was this: Into a tap-water hanging-drop culture of *R. reticulata* fragments and isolated gonidia, obtained in the way described on page 218, I introduced by sterilized platinum loop a number of germinated spores, stirring gently so as to mix the spores with the gonidia. Germinated spores were thus brought close to isolated and apparently healthy gonidia. One would naturally expect the germ-tubes to be chemotropically attracted by the gonidia and to bend towards them. As illustrated by fig. 4, the hyphæ put forth by the spores did not bend at all. The hypha figured was about half as long when the germinated spores were sown in the gonidia culture. It continued to grow straight on, did not branch, and never united with the adjacent or with any other gonidium. The same is true of all the others, and although I kept the preparations until all the gonidia were evidently dead, though the hyphæ still looked healthy, no union of hyphæ and gonidia took place. Undoubtedly the bacteria, which overran these cultures within a week after they were made, are responsible for the failure of the gonidia to attract the hyphæ, of the hyphæ chemotropically to respond, and of the two to form a new lichen. That the failure of the attempts just described is not due to an unhealthy condition of the gonidia produced by the isolation is proved on page 220.

DeBary (1887) reports from Stahl's (1877) investigations on the formation of the lichen-thallus, that "smaller branchlets are formed at the points of contact" of the hyphæ with an algal cell, which closely embrace it and enclose it in fresh ramifications. Whether actual contact is necessary, whether the gonidia stimulate the germ-tubes to bend or to branch, whether the union of gonidium and hypha is always by branches of the germ-tube and not by the tube itself — these are questions which renewed investigations only can answer. When, by greater skill and better methods than I have possessed, one is able to put together isolated healthy gonidia and healthy germinated spores, in hanging-drop cultures free from bacteria, the formation and growth of the lichen can be followed, step by step, from the chemotropic behavior of the germ-tubes to the complete investment of the gonidia by the fungus.

III. THE RELATIONS OF GONIDIA AND HYPHÆ AS SHOWN BY CULTURES.

Although I have been unable to reconstruct a lichen, still I believe that by other means I have obtained some information regarding the questions which I hoped to answer in that way.

To isolate the gonidia of *R. reticulata* without injuring them is a matter of considerable difficulty owing to their position in the compact thallus. The methods described by others do not lend themselves to the species upon which I have worked. Baranetzky (1869) apparently made no attempt to isolate the gonidia from the hyphæ directly, contenting himself with making thin hand-sections of living lichens (*Collema*, etc.), and placing them in moist chambers. The result was that the gonidia multiplied and grew more rapidly than the hyphæ, coming out upon the upper surface of the sections and accumulating there practically free from hyphæ. Such a method as this, though satisfactory with filamentous gonidia in lichens of comparatively loose texture, is ill suited to lichens of close texture, containing spherical gonidial cells (*Cystococcus*, *etc.*) The gonidia do not become free under these conditions. The reason for this may lie in the absence of intracellular haustoria in Baranetzky's lichens and in the close investment and the penetration of the gonidial cells by the hyphæ of the lichens which I have studied. The gonidia of the latter seem to be too completely in the power of the hyphæ to be liberated in this way.

Teasing out thin sections in water by needles is a slow, tiresome and unprofitable task, for even in this way it is almost impossible to break up the small groups of gonidia closely invested and penetrated by hyphæ. These little masses placed in cultures behave like lichens, growing almost imperceptibly; the gonidia do not grow and multiply rapidly and so disrupt the little groups and escape to the surface.

When air-dry, *R. reticulata* is tough and leathery, difficult to section, readily bent, but not at all friable. Sections of the air-dry thallus cannot be pulled to pieces dry by needles, and, when placed in a drop of water on the slide, expand without at all loosening the hold of the hyphæ upon the gonidia. Teasing out sections cut dry and then placed in water is as unsatisfactory as though the sections were cut from a moist thallus.

The toughness of the thallus is due to the longitudinal direction and the compact arrangement of the rather thick-walled hyphæ near the surface. The surface is soft and gelatinous when moist, hard when air-dry. The gelatinous matter of the outer portions of the thallus both holds water very strongly and takes it up very quickly. Air-dry at the end of the long dry season, the lichen still contains 13.9 per cent. of water or nearly one-seventh of its weight, as shown by the following figures:

Weight air-dry	4.72	gr.
Weight constant at..	4.06	gr. when dried several hours at 90° C.
Weight lost	0.66	gr.
Percentage of water.	13.9	

The dried lichen must be weighed quickly, for it rapidly absorbs moisture from the air and returns to its original weight. When absolutely dry it is as brittle as it ordinarily is tough, and it may be ground in a mortar to a fine powder. Microscopic examination of this powder in water shows it to consist of minute fragments of hyphæ interspersed with isolated gonidia apparently uninjured by the grinding. It occurred to me to attempt drying the lichen at a temperature low enough to avoid injuring the gonidia. Warming in an oven for five hours at 36° C. (96° Fahr.), a temperature often attained, and sometimes maintained for several hours, on a summer day, proved to be perfectly harmless to the gonidia, but it did not dry the lichen to the point of brittleness. To attain brittleness without further heating, small pieces were kept for four days in a desiccator containing glacial phosphoric acid. Even after this treatment the fragments were not perfectly dry and brittle, though grinding rapidly in a mortar yielded powder of which the finest part contained isolated and apparently uninjured gonidia. Some of this was inoculated by needle into hanging drops of sterilized tap-water.

The individual behavior of the isolated gonidia, fairly scattered throughout the hanging drop, could be easily followed. Many of them were entirely free from any trace of hyphæ, while some had short pieces of hyphæ still attached to them. Of the latter, some gonidia, as shown by fig. 12, had haustoria in them, while others appeared to have the hyphæ only adhering or attached to the outside (fig. 7). A difference in size and in subsequent behavior between those gonidia absolutely free from the fungus, and those upon which and in which fungus fragments still remained, is to be noted. Those gonidia which, though enclosed within the lichen, have not been invested by fungus hyphæ, still less penetrated by haustoria, are larger, deeper green, and in every way healthier looking than the others. How is this to be accounted for?

The enclosed but not invested algal cells seem to me to be the only ones in the lichen thallus which are at all advantageously situated. They do have a more constant supply of aqueous solutions of food materials than their fellows outside, they are shaded from excessive light, screened from excessive heat, protected from excessive dryness, shielded perhaps from sudden changes of any kind, possibly manured by the excreta of the fungus. In these ways they may be better off than their unhoused fellows, and sometimes at least they are larger. They are not subject to the drain upon their vital energies which those gonidia invested and penetrated by hyphæ must withstand if they are to survive. The fungus can obtain from these gonidia with which it is not in permanent and intimate contact only such substances as diffuse from them into the water of the lichen-body; whereas it can withdraw through a haustorium within the cell, and even through the cell-wall with which a hypha is closely in contact, the foods elaborated by the gonidia for their own use. Gonidia not invested by hyphæ are to be found in every preparation. They are conspicuous from their larger size, deeper color and generally healthier appearance. It may have been these which suggested the notion that green cells are better off as gonidia than as independent algæ.

The next difference to be noted between the invested and uninvested gonidia is in their subsequent behavior in culture. Within a very few days (at the utmost six) the gonidia which contain haustoria, or which have hyphal fragments still attached to them, have either divided by internal cell-division at least once, or their cell-contents have contracted away from the wall. Figures 6, 7, 8, 9 show various stages in the division of invested gonidia, in fig. 6 into two, in fig. 7 into four, in fig. 8 another divided into four, in fig. 9 at *a* the same cell twenty-four hours after, when the wall of the mother-cell had become dissolved, setting free eight daughter-cells. In fig. 9 at the *, and in fig. 10, we have gonidial cells in which the haustoria, broken away from the hyphæ which formed and bore them, are plainly visible, the contents of the gonidial cells contracting away from, and in in this way escaping, the haustoria. Later the contracted mass surrounds itself by a new wall and behaves like the uninvested gonidia. These last do not divide in the culture for a very long time.

The only difference between the invested and uninvested gonidia in the culture being in their relation to an organism incapable of manufacturing its own food, it can be safely concluded that the cell-contents of the former divide, or contract away from the wall, in order to eliminate the foreign organism, and to produce individuals which will be free from it. The conditions prevailing in a hanging-drop culture cannot be entirely favorable to the green cells; if they were, all the gonidial cells would sooner or later divide. Haustoria within, or hyphal branches closely enwrapping them, must irritate the invested gonidia. The response to this irritation is an effort to get rid of it by contraction or by division. The uninvested gonidia, not subjected to this irritation, do not contract or divide.

The gonidia of *R. reticulata* are in rounded masses fairly compact and held together by hyphæ (figs. 5 and 11, and Peirce [1898], p. 412). Many of these masses are composed of small cells, and some of the cells are likely to be dividing internally (figs. 6 and 9). From such divisions there result new gonidia, but it is not necessary to infer, as some do, that the gonidia are thus only amiably doing their part toward the growth and the permanence of the lichen. On the contrary, as Hedlund (1895) describes for *Catillaria denigrata* (Fr.) and *C. prasina* (Fr.), and as I have just shown in the above, we have in both cases merely the attempt on the part of the gonidia to divide in such a way as to exclude the haustoria from as many of the daughter-cells as possible. That the gonidia cannot be benefited, but are evidently injured, by having haustoria within them, I shall show subsequently (page 226); and if the haustoria are injurious, is it not sensible to suppose that the gonidia will try to get rid of them? If they are harmless or beneficial why should there be frequent divisions which inevitably result in the formation of daughter-cells free from haustoria? In a culture, the conditions in which seem to be more favorable to the uninjured gonidia than to the much broken and greatly injured hyphæ, the gonidia succeed in eliminating the haustoria and in freeing themselves from enclosing hyphæ. Imbedded in the body of the lichen, surrounded on all sides by hyphæ, the advantage in the struggle is to the other side; but the struggle and the manner of it are the same. The gonidia in the lichen seek by division to escape the hyphæ. Some do — these flourish and grow large; most do not — these divide again as soon as possible and so remain small.

IV. THE RELATIONS OF GONIDIA AND HYPHÆ AS SHOWN BY MICROTOME SECTIONS.

So far as I know, very little use has been made of modern cytological methods in the study of lichens. This is to be regretted, for without recourse to these, the intimacy of the relations of gonidia and hyphæ must remain comparatively obscure. It has already been demonstrated that our culture-methods are still so defective, and the growth of the fungus-component of lichens is so distressingly slow, even under the most favorable conditions, that our knowledge of lichens, if it is based on hand sections and cultures only, must be incomplete. Hand sections are unsatisfactory at the best because they are so thick that important details are hidden by excess of material. Yet investigations of lichens which are based only on examinations of dead herbarium material, or even of freshly fixed, imbedded and sectioned specimens, are subject to the same danger of one-sidedness which sometimes threatens the work of those who know plants and animals only as embalmed tissues.

It is deplorable that we are still utterly unable to obtain, and to keep healthily alive, thin sections of living material. As Fischer (1895) and others have repeatedly emphasized, a technique which is based on the employment of poisonous acids and salts is one which can be implicitly trusted only when their effects on the living protoplasm are exactly known. The danger of being misled by the study of fixed material sectioned by microtome after imbedding is, however, minimized by examination of living material, both sectioned and in culture, as a control. When the question before the student can be answered in part at least by determining the relative position of cell-walls, nuclei, etc., the matter is still simpler. Such is in great measure the case with the questions which are under discussion in this paper. From microtome sections of lichens it is possible to obtain clearer views on the structural relations of hyphæ and gonidia than can be had otherwise, and from these data, supplemented by culture experiments, conclusions regarding their physiological relations may safely be drawn.

As reported elsewhere (Peirce, 1898*a*), the material was prepared as follows: freshly collected specimens of *R. reticulata*, *Sphærophorus globiferus* (L.) D.C., and an *Usnea*, after being thoroughly wet, were kept in a moist chamber near a window for twenty-four hours. This allowed the gonidia to resume their photosynthetic activities in the light, and the hyphæ to become reasonably plump, if they had become dried out of doors.

For fixing I used:

Chromic acid, 3 per cent., at room temperature.
Chromic acid, 1 per cent., just below boiling temperature.
Flemming's Chrom-osmic-acetic mixture, at room temperature.
Corrosive sublimate, saturated solution in 35 per cent. alcohol, at room temperature.
Corrosive sublimate, saturated solution in 35 per cent. alcohol, just below boiling.

The last proved the most successful. Penetration at room temperature is comparatively slow, owing to the large amount of air enclosed in even wet lichens, whereas the air is quickly driven out by the hot liquid. At room temperature, the fragments treated with the fixing agent float, and must be exhausted under the pump. Those treated with the hot fixing-solution sink in it almost immediately. There is, therefore, a saving of time, as well as greater certainty of rapid penetration, if the fixing agent is applied hot. Dehydration should not be carried on too rapidly, for the gelatinous walls, especially of the outer hyphæ, hold the water. After complete dehydration, the material was transferred from absolute alcohol to equal parts absolute alcohol and xylol, then to pure xylol, and to this were slowly added small fragments of paraffin melting at 55°. At the same time the temperature was slowly raised to about 40°. Paraffin was then added to the point of saturation and the xylol allowed to evaporate. When the xylol was driven off, the specimens were transferred to melted hard paraffin (melting-point about 59°), kept in this for two hours to remove the last trace of xylol and to insure perfect penetration, then blocked, and sectioned at leisure.

The gelatinous hyphæ, soft and easily cut when wet, are now hard and rather brittle. For very thin sections, and these yield the most trustworthy results, the knife must be even sharper than for most tissues. The best sections were 1 μ thick, made with a Zimmermann-Minot microtome, and fastened to the slide, after floating and straightening on warm water, by albumen fixative. Some were then stained with Czoker's Alum-Cochineal and Bismark Brown. Some material was stained *in toto* with the Cochineal, but this was less satisfactory than staining on the slide. Other sections were stained with Iodine-green-Fuchsin, washing out with Iodine in 80 per cent. alcohol, and still others with Anilin-safranin-Gentian-violet-Orange G., according to the directions given by Zimmermann (1893). Both of the double stains and the triple stain were very satisfactory in their different ways. The sections were examined with a Zeiss apochromatic 2 mm. oil-immersion objective and compensating eye-pieces 6 and 12. All of the drawings were made with Abbé camera.

Various gonidial cells of *R. reticulata* containing haustoria are shown in section in figs. 11, 13, 15. Figures 12 and 14 were drawn from isolated and not from sectioned gonidia, but, for the sake of comparison, they may be referred to here. Figures 11, 12 and 13 show gonidial cells into which the haustoria can have penetrated only comparatively recently, as the protoplasm and chromatophores are apparently perfectly normal and uninjured. Figures 14 and 15, on the contrary, are of gonidial cells completely emptied, in which the haustoria still remain, normally plump and with granular protoplasm. Figures 13 and 15 show the haustoria in profile, figs. 12 and 14 end on. In fig. 13, the haustorium, and the hyphal cell of which it is a branch, are shown to be continuous as to both wall and cavity. Figure 15 shows the haustorium within the cell, but the hyphal cell of which it is a branch was below the plane of the section. This gonidial cell was invested by a larger number of hyphæ than any other figured, and than the great majority of those examined. In the group of gonidial and hyphal cells shown in fig. 11, two gonidial cells show haustoria within them.

It is nothing new to find haustoria in the gonidia of lichens. They have been repeatedly seen and sometimes figured, perhaps most strikingly by Schneider (1896*a*). It is generally said, however, that the haustoria, though penetrating the walls of the gonidial cells, do not actually penetrate the protoplasm. Thus Hedlund (1895)—"Von der Seite einer Hyphe wächst ein kruzer Ast heraus, der die dünne Membran vollständig durchbohrt und innerhalb derselben mehr oder weniger kugelförmig anschwillt. Bei dem Eindringen der Hyphe zieht sich die Hautschicht des Protoplasmas zurück und bildet eine seichte Einbuchtung, in welcher das angeschwollene Haustorium seinen Platz hat —" and Schneider[1]—" The tip of the haustorium may pass through the algal cell-wall, forming a somewhat expanded filament between the wall and cell-plasm. In its highest development the haustorium, often entering the algal cell, develops a much branched network which encloses but does not penetrate the cell-plasm."

Neither in my sections, nor in the living gonidia, in which I found haustoria, could I detect the alleged "Einbuchtung" of the protoplasm, and certainly the haustoria do penetrate the protoplasm of the gonidial cells of *R. reticulata*, as the figures convincingly show. It may be that, at the time of penetration, the protoplasm may contract away from the intruding haustorium, but this condition is not permanent, the haustorium penetrates the cell, the essential and living part of the cell, as certainly as it penetrates the lifeless cell-wall.

Can one imagine that the presence of another body, whether living or lifeless, within the living protoplasm of a cell is not accompanied by profound disturbance of the living protoplasm, is not distinctly irritating to it, is not positively injurious to it? The contrast between the evidently healthy hyphæ and haustoria on the one hand, and on the other the haustoria-containing gonidial cells, many of which in sections and in free preparations had contents dead and shrunken or completely gone, at least suggests very strongly, though it does not prove, that the haustoria completely devour the contents of the gonidia.

It does not necessarily follow that the penetration of chlorophyll-containing host-cells by haustorial cells is fatal to the host-cells. This is the case, for example, in the host-plants of *Cuscuta* (Peirce 1893), but no one would venture to intimate that this phanerogamic parasite, containing traces of chlorophyll and therefore less incapable of elaborating non-nitrogenous food than any fungus, does not distinctly injure every cell into which its haustorial cells penetrate. In the lichen, each green cell penetrated by a haustorium is obliged to manufacture non-nitrogenous food in quantity sufficient to supply both the haustorium and itself, and not only for the haustorium but also for the cell of which it is a branch and for the cells adjacent to it. How long can a green cell do this unusual amount of work? Certainly not for so long as it could do less work. The life of the individual cell is therefore shortened. Overwork, exhaustion, death, and finally the complete absorption of its contents, follow the penetration of a haustorium. Is the presence of the haustorium so beneficial or so pleasant as to compensate the gonidial cell for its increased work and and decreased span of life?

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[1] l. c., Pl. I and p. 445.

Turning once more to *Cuscuta* and its host for comparison, we find that both host and parasite are multicellular, that owing to the division of labor among the cells one cell can help another. For instance, if the photosynthetic or other food-elaborating activity of a green cell is reduced by the intrusion of a haustorial cell, the former will be supplied by its neighbors, in accordance with the laws of diffusion and osmosis, with those substances which it lacks. This is an inevitable physical as well as a regular physiological phenomenon, the result of the multicellular condition of the host. Thus the life of the penetrated cell, fed by its neighbors, may be prolonged; the struggle between host and parasite is more nearly equal, each haustorial cell draws upon more than one cell of the host to supply the more than one cell of the parasite. This last is also true of the fungus in the lichen, for there are many gonidial cells. But the gonidial cells are distinct from one another; the fungus is a multicellular plant, with the advantages of one; the gonidia — *actually* in *Ramalina* and in many other lichens, *virtually* in all — are unicellular plants with their corresponding disadvantages. The single gonidial cell must do everything itself or perish. The individual gonidial cells penetrated by haustoria are no better off as individuals than algal cells of the same species outside the lichen: they are obviously worse off.

Beside the gonidial cells penetrated by haustoria, there are a much larger number, to be seen both in sections and in free preparations, which are invested more or less closely either by the hyphæ themselves or by short branches therefrom. These last Schneider (1896*a*) calls "extra-cellular haustoria." The true haustoria, of which we have just been speaking, he terms "intra-cellular haustoria." Both are branches of hyphæ, are therefore morphologically the same; both are organs of nutrition, are therefore physiologically the same; but it seems hardly desirable to give to organs which do not penetrate, but only clasp, the same name which DeBary (1884) and so many after him have used with the original meaning only—"in's Innere der Zellen dringende Seitenzweige."

Whether we have to do with naked or enclosed masses of living protoplasm, their absorption of food is by the same means—by osmosis. The osmotic absorption of aqueous solutions of food substances into cells enclosed by thin cellulose walls is nearly if not quite as rapid as with naked cells. Through a thick cellulose membrane or through two cellulose membranes which, though closely applied to one another, are thicker than only one, osmosis is slower than through a thin cellulose membrane. Through a gelatinized membrane osmosis is also slower than through a cellulose membrane of the same thickness (Pfeffer 1897). From these considerations we see the means by which both the haustoria penetrating, and the hyphal branches investing, the gonidial cells obtain from them the nutrient solutions which the fungus must obtain from them or die. If the hyphæ become gelatinized as to their walls, their absorption of food will be diminished equally with their loss of water. The production of haustoria will, therefore, facilitate the absorption of adequate amounts of food. In many lichens, however, haustoria are never formed; the hyphal branches investing the gonidia osmotically absorb enough food to supply the whole body of the fungus. The principles underlying the absorption, and the results of the absorption, of food by the hyphæ from the gonidial cells are identical whether haustoria penetrate or hyphal branches only clasp the gonidial cells.

Microtome sections confirm the observations regarding the relative sizes, the number and kinds of division, the general appearance of the gonidial cells invested by and free from hyphæ, as reported in the foregoing chapter. Both the fixed and the living specimens show that fungus and alga are associated intimately enough, whether the fungus merely encloses or actively penetrates, for the organism absolutely unable to elaborate non-nitrogenous food to be able to absorb all that it needs from the one that can elaborate it. In both cases the absorption is by osmosis, and it must be almost, if not quite, equally effective in both cases, for the lichens which do not send hyphal branches as haustoria into the gonidia appear to thrive as well as those which do.

There must in both cases be irritation of the gonidial cells by the hyphæ. The irritation produced by haustoria must, however, be greater, and this conclusion is substantiated by the larger number of dead gonidial cells containing haustoria than of those with hyphæ merely attached. The observation of haustoria within gonidial cells, though not a step necessary to the conclusion that the fungus is parasitic upon the alga, is confirmatory evidence, for it proves that the fungus has the alga in its power — that it obtains all its food from it, that it irritates and exhausts it in proportion to the intimacy of its relation with the alga.

In the other two forms studied — *Sphærophorus globiferus* and an *Usnea* — microtome sections show that the relation between hyphæ and gonidia is intimate, the hyphæ closely investing the gonidia. Figure 19 is from a section through an old part of a *Usnea*, the species of which I did not determine, and shows a hypha, old and thick-walled, still closely applied to a gonidial cell which has begun to divide. Figure 20 is from a similar section of *Spærophorus* and demonstrates the intimacy of contact between the hyphæ and a gonidial cell also dividing. I did not succeed in finding haustoria in these two lichens, but from the closeness of the contact which, as these two figures show, exists between hyphæ and gonidia, and from the foregoing discussion of the physiology of this relation, one is certainly justified in concluding that the fungus and the alga stand to each other, in these two lichens as in *Ramalina*, in the relation of parasite and host. The algæ in these three lichens are the same, *Cystococcus humicola*, Näg.[1] It would be interesting to compare with these forms lichens which have other species of algæ as gonidia, but for various reasons I prefer to leave this to others or to later work of my own.

V. THE SIGNIFICANCE OF THE WATER-CONTENT OF *Ramalina reticulata*.

The amount of water held, and the force with which it is held, even in very dry air, is significant. The lichen cannot die from drought, and the alga is defended against extreme dryness by the gelatinous enveloping fungus, which holds water enough at least to keep the alga alive, and probably enough to enable it to elaborate some food each day. It is hard to conceive that the alga, supplied with any moisture at all, should be entirely inactive when daily illuminated by the sunlight; and owing to the affinity of the gelatinous outer hyphæ for water, the dews and the frequent fogs at night must furnish as frequent additions to the water-content of the lichen. It seems extremely probable, therefore, that the long dry season of California, checking the growth and many other activities of most plants hereabouts, is not sufficiently dry to stop the photosynthetic and other activities of the gonidia of this lichen, much less to kill them; and hence the hyphæ, well supplied with food, may also, at least frequently, be active in growth and in other ways. For twelve months in the year these lichens can, and undoubtedly do grow, though the most rapid growth and the most growth must be during the warmer later part of the rainy season.

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[1] Professor William A. Setchell, of the University of California, kindly informs me that this alga is now commonly called *Chlorococcum humicola* (Rab.) Näg.

If this is the case with the lichen as a whole, what is the condition of those free algal cells entirely away from and uninvested by fungus hyphæ? Throughout a normal dry season on the west side of the Bay of San Francisco, the fogs at night and the dews are sufficiently frequent and heavy to wet fences, tree-trunks, branches, etc., etc. Though this moisture evaporates quickly after the sun appears, I doubt very much that *Cystococcus*-like algæ are so completely dried by day that they do not revive at night. Indeed, spherical unicellular algæ, *Cystococcus*, *Protococcus*, etc., although less abundant here on tree-trunks, fences, etc., than in many other parts of the world, can be found alive at all seasons. On almost every fence old enough, one may find the algæ alone, or with a few hyphæ among them, or with more but still not enough to cover and shield them from dryness, and so on up to mature and fruiting lichens of various species. In this region, at least, the survival of algæ like those in lichens is not dependent upon their being protected by fungus hyphæ against extreme dryness.

It is argued that because lichens are found flourishing where algæ alone could not possibly survive — for instance, on dry and sun-baked rocks — that this is evidence that the association of alga and fungus is mutually beneficial. Concerning this, *R. reticulata* offers a case in point. The algæ forming the gonidia of this pendant lichen could not possibly remain alive in the air even if they could float in it. Yet, is it any advantage to the gonidial cells of this lichen that they are living, growing, multiplying, where the force of gravitation and the insufficiency of food would forbid algæ free from fungus associates to survive? The answer to this question will be clearer if we use a homely analogy. A cow would never climb to the top of a twenty-story building, but once elevated to this position in opposition to her ordinary habits and to the force of gravitation, would she be any more advantageously placed than her more commonplace relatives in barn and pasture? Though algal cells cannot suspend themselves in mid-air, or live indefinitely exposed to excessive heat and dryness on sun-baked rocks, it does not necessarily follow that they are any better off when associated with fungus hyphæ and contributing to the formation of a lichen, than are their more commonplace relatives which are not in the air and have fallen on more advantageous places than exposed rocks.

VI. THE INFLUENCE OF MECHANICAL STRAINS ON GROWTH.

As reported in a previous paper on *R. reticulata* (Peirce, 1898), the mere wetting of a thallus or thallus fragment, and the subsequent drying, bring about no material change in the length, breadth or thickness. During the rainy season, however, when the lichen remains wet for considerable lengths of time, growth will take place while the lichen is expanded and soft, thus permanently increasing the dimensions. The lichen will not contract, when it dries again after the rainy reason has passed, to the dimensions it possessed when the rains began; but how much of this increase in size is due to growth solely, and how much to stretching and the consequent change in position of the hyphæ, cannot now be stated. It is obvious that this pendant lichen, being more than twice as heavy (Peirce, 1898), as well as much softer, when wet than when dry, will be subjected in its different parts to a stretching force varying in the different parts with the weight of the parts nearer the tips. The parts nearest the branch from which it hangs will be subjected to the greatest stretching force or weight, the tip to the least. By stretching force I mean in this connection not the forcible expansions which follow the wetting and consequent swellings of a dry lichen, but the actual stretching strain which the distal parts exert by their own weight upon the basal upper parts, a strain which increases with the wetness and with the actual increase in substance. Once thoroughly wet, the lichen will not absorb still more water, but it may grow. We must distinguish, then, between growth which, in this connection at least, is a purely physiological process, and stretching, which is a purely mechanical one. The growth involves an increase in the size of the cells composing the lichen, is made possible by accumulated foods elaborated by the gonidia and hyphæ, and is very quickly followed if not accompanied by an actual increase in the weight as well as in the volume of substance either itself living or at least elaborated solely by the living substance.

The pull exerted upon itself by the wet and heavy lichen is parallel with the long axis of the thallus; it is stretched lengthwise, while growth takes place in breadth and thickness as well as in length. Hegler (1893) has shown for higher plants that a pull exercises two distinct influences; the mechanical one of stretching, the physiological one of irritating — a pull entirely insufficient for the former being in many cases quite sufficient for the latter. The irritation produced by pulling retards growth in the direction of the pull, stimulating it in other directions both as to the individual cells and also as to the tissues and organs as a whole. A pull so light that it does not stretch a stem or branch will lower the rate of elongation, raise the rate and degree of thickening of the walls, especially of those cells which contribute most to the mechanical strength of the plant, and in proportion to the actual increase in length there is more than the usual increase in diameter, by thickening the walls of already existing cells as well as by inducing the formation of new cells.

Without having made any measurements — a matter requiring infinite patience on account of the low rate of growth and because of the many sources of error to be eliminated — and merely from a study of the structure of this lichen (Peirce, 1898), I think we may justly infer in the light of the foregoing discussion, that the increase in length of *R. reticulata* is due in greater measure to that stretching of the thallus, by its own weight, which results in bringing the hyphæ from their diverse directions into a course nearly parallel with the long axis of the thallus (i. e., parallel with the pull) than to actual growth. The physiological process of growth in length, made less necessary if not retarded by the mechanical pull to which this lichen is constantly subject — a pull which is greater when the lichen is softest and weakest — is accompanied by growth in breadth and in thickness and by an increase, by thickening walls, in the mechanical strength of the hyphæ. These processes are at least not hindered and, judging from Hegler's work on higher plants, are likely to be stimulated by the longitudinal pull. As a result of the growth in thickness and breadth, the normal proportions of the thallus will be maintained and, furthermore, more hyphæ will be formed which, running at various angles to the long axis, may by the pull be drawn into courses parallel with it.

But Hegler has shown one other thing interesting in this connection, namely, that changes in the pull also affect the rate of growth, and that if the pull remains constant for a time the plant will recover its normal rate of growth in length, growing in diameter and increasing in mechanical strength in proportion to the force to which it is subjected. The decreasing weight of our lichen on drying, the gradual diminution of the pulling force, will stimulate it to some growth in length; but because the lichen stiffens as it dries, it cannot grow much at this time, and hence one can conceive of little more growth taking place than will suffice to fix the hyphæ in the direction into which they have been pulled. Since the pull does not remain constant in nature, winds and varying amounts of moisture forbidding this, the lichen cannot become accustomed to any one amount of force, cannot resume its normal rate of growth if, indeed, it may be said to have any one normal rate, though it must and does have normal rates.

VII. NUCLEUS OR PYRENOID AS THE CENTRAL BODY OF CYSTOCOCCUS CELLS.

There remains one more point to be discussed in this paper. In two papers which I have been unable to see but which are briefly reviewed in Just's Jahresbericht (Bd. XXII, 1, p. 148), Dangeard (1894) claims that the body generally regarded as the nucleus of gonidial cells is not nucleus at all but a pyrenoid, the real nucleus being at the side, small, inconspicuous, and formerly supposed to be a vacuole. Differential staining agents are alleged to prove Dangeard's assertion. As the species of gonidia investigated by Dangeard are not mentioned in the review, I cannot criticise his results and can only advance evidence to show that the central body in the cells which serve as the gonidia of the lichens reported upon in this paper, is certainly a nucleus, as the well known nuclear stains and the phenomena of division and cell-division plainly indicate. In a spherical cell, too, one would certainly expect to find the nucleus near if not at the center of the cell under ordinary conditions. In no case have I found a nucleus-like body far from the center of the gonidial cells of the lichens which I have studied. One would expect the nucleus to have the size in proportion to the diameter of the cell which this central body possesses, and not to be small, eccentric and inconspicuous. The form of the nucleus would be likely, for mechanical reasons, to approach that of the cell, though of course this is by no means always the case even in spherical cells. Pyrenoids occur always in chromatophores, as specially differentiated parts of them, not as independent organs.

In fig. 16 we have a typical gonidial cell in a thin microtome section of *R. reticulata*, stained on the slide with Iodine-green-Fuchsin. The central body, enclosed in cytoplasm in which the large rounded chromatophores are imbedded, is dense, granular and provided with a central homogeneous body of its own which, like nucleoli in general stained with this agent, has a deep red color. Figure 17 shows a gonidial cell in the same section in process of internal cell-division. For the sake of clearness, protoplasm, chromatophores and vacuoles are omitted from the drawing. Each daughter-cell, though not yet provided with its own cellulose wall, contains a dense, granular central mass, from which the nucleolus-like body is absent. This is what one would expect if the central mass is nucleus, for the nucleoli ordinarily disappear before division, reappearing in the daughter-nuclei only after the lapse of some time. Figure 18 is still another gonidial cell in the same section, which has divided still further, the eight daughter-cells, most of which are below the plane of the drawing, being already surrounded by their own cellulose walls and each containing its own central body.

From these figures, from the behavior of the nucleolus-like body both toward the stain and also in division, from the different staining of the central body, the cytoplasm and the chromatophores, and from its position, as far removed as possible from all the chromatophores, I cannot do otherwise than conclude that it is a nucleus.

Figures 19 and 20 show the nuclei of a gonidial cell of *Usnea* sp. (?), and of *Sphærophorus globiferus*, respectively, dividing and divided. These figures were made from thin microtome sections stained with Anilin-safranin-Gentian-violet-Orange G. The colors, though faint, differentiate nucleus and cytoplasm in the manner characteristic of this stain.

From the evidence it seems to be clear that the gonidia of these lichens have a central nucleus neither remarkable nor different from the nuclei of other similar algæ whether within or outside of a lichen thallus; that this nucleus is provided, in the "resting condition," with a typical nucleolus which disappears before the division of the nucleus and the cell; that nuclear division precedes cell-division. As to additional details of the processes of nuclear and cell-division, the small size of the objects makes study very difficult, and because this has no direct bearing on the main problem discussed here, I leave the matter as it now stands.

VIII. SUMMARY.

The results of this examination of a few forms, though admittedly of too few and too like forms to justify anything more definite than an opinion regarding lichens in general, may still be of value as a contribution to the discussion of the relation of fungus and alga in lichens and of the so-called autonomy of lichens. These results may be briefly stated as follows:—

I. Both cultures and thin microtome sections demonstrate
  1—that hyphæ and gonidia are in the most intimate contact;
  2—that the hyphæ develop branches which may merely clasp the gonidial cells or may, as definite haustoria, penetrate them;
  3—that such clasping or penetration stimulates the gonidia to internal cell-divisions in the effort to form individual cells free from hyphal investment;
  4—that the haustoria consume the protoplasmic contents of the gonidial cells which they have entered, leaving only the empty cell-wall.

II. 1—Since the fungus, being devoid of chlorophyll, must obtain already elaborated non-nitrogenous food;
  2—since the only constituent of the lichen capable of elaborating non-nitrogenous food is the gonidia;
  3—and since lichens ordinarily grow where they could obtain little or no non-nitrogenous food from the substratum even if they were dependent upon it for other than mechanical support and mineral salts,—it is obvious that the fungus is fed by the alga; the hyphæ, by the gonidia.

III. Though algæ may not always grow independently where they are found associated with fungi, forming lichens, it is neither logical nor sensible to conclude that their unusual position is beneficial to them.

IV. Though the percentage of water retained by the more or less gelatinous constituents of the lichen thallus is higher than that which the gonidia could retain as free organisms, the occurrence of healthy algæ on the spots subsequently occupied by lichens demonstrates that free algæ can thrive, at least for a time, wherever lichens can.

V. Though it may be claimed that the individual gonidial cells live longer in the lichen than the free individual cells of the same species of alga, there is no proof of this, and if there were, it is well known that in their resting forms free algæ withstand extremes of heat, dryness, etc., as successfully as do lichens and lichen gonidia.

VI. There is no proof that algal cells serving as lichen gonidia are any better off as to food, protection or situation than the average free algal cells of the same species; whereas it is evident that the fungus portion of every lichen is absolutely dependent upon the gonidia for all of its non-nitrogenous food.

VII. As to Reinke's claim that the lichens should be regarded as plants as truly autonomous as trees and shrubs because they have their own peculiar structure, growth, habit, color, etc., as well as because there can be no lichen without both components, an analogy may assist us to clearer views. Bacteria grown in bouillon cannot form the definite colonies of peculiar and characteristic structure, growth, habit, color, etc., which the same species will form on nutrient agar-agar or gelatine. To the formation of the colony, with its characteristic peculiarities, the living bacteria and the lifeless but nutritious solid substratum are both absolutely necessary. The bacteria may grow quite as well in a liquid medium as upon a solid one, but they will not aggregate into the same form. So the fungus component of a lichen, grown by Möller on liquid media and alone will not form a body like a lichen in structure, growth, habit, côlor, etc., although it will develop perfectly well. Both substratum and associate will affect the fungus, and *the lichen is the product, the resultant, of all these influences, not of one or two.*

VIII. The varying mechanical pull exerted by itself and by the wind upon *R. reticulata* influences its growth in the three dimensions of length, breadth and thickness.

IX. The central body of the gonidial cells of *Ramalina*, *Usnea*, and *Sphærophorus*, which are *Cystococcus humicola* Näg., is a nucleus, not a pyrenoid.

STANFORD UNIVERSITY,
CALIFORNIA,
December, 1898.

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EXPLANATION OF PLATE XLI.

The figures were drawn with Abbé camera over Leitz No. 7, or Zeiss 2 mm. apochromatic oil-immersion objectives, and Leitz eye-piece 3 or Zeiss compensating eye-pieces 6 and 12.

Ramalina reticulata.

Fig. 1, *a* and *b*. Ungerminated spores in water: *a*, smaller than the average and probably unripe; *b*, larger than the average. x 1300.

Fig. 2. Germinated spores, showing breaking up of the oil drops and their re-formation in the germ-tubes; both cells of each spore germinating. x 1300.

Fig. 3. Germinated spore; only one cell putting out germ-tube, but this branched. x 1300.

Fig. 4. Germinated spore; germ-tube growing close to and straight past a healthy gonidium. Is actual contact needed to produce stimuli? x 650.

Fig. 5. Group of invested gonidia and one uninvested gonidium separated by grinding; showing relative sizes of attached and unattached gonidia. x 650.

Fig. 6. Group of invested gonidia set free by grinding; showing gonidia dividing internally into two. x 560.

Fig. 7. An invested gonidial cell dividing into four. x 560.

Fig. 8. A similar one showing four enclosed daughter-cells. x 560.

Fig. 9*a*. The same cell as fig. 8, twenty-four hours later, showing eight daughter-cells liberated by solution of wall of mother-cell. x 560.

Fig. 9*. A gonidial cell containing a haustorium; the protoplast contracting and thereby escaping from the haustorium. x 560.

Fig. 10. Similar to fig. 9*. x 560.

Fig. 11. Group of invested gonidia, showing two haustoria within gonidial cells. x 650.

Fig. 12. Isolated gonidium containing haustorium; gonidium isolated and hypha broken off by grinding. x 1750.

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Fig. 14. Gonidium, isolated by grinding, entirely emptied by haustorium. x 1750.

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Fig. 16. Unusually large and healthy gonidial cell, free from investing hyphæ and showing chromatophores enclosed in peripheral cytoplasm; the central nucleus with its nucleolus and enclosing cytoplasm with radiating strands. x 1750.

Fig. 17. A gonidial cell dividing by internal cell-division into four daughter-cells, each with its own central nucleus; daughter-cells not yet surrounded by their own cell-walls. x 1750.

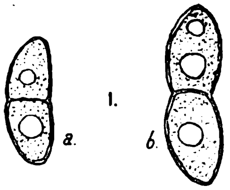
Fig. 18. Gonidial cell divided by internal cell-division into eight daughter-cells, each with its own central nucleus and its own cell-wall. x 1750.

Usnea.

Fig. 19. The central body, nucleus, of a gonidial cell dividing, preliminary to the division of this invested gonidial cell. x 1750.

Sphærophorus globiferus.

Fig. 20. Somewhat later stage in the division of the central body, nucleus, of an invested gonidial cell. x 1750.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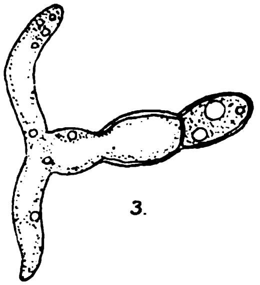
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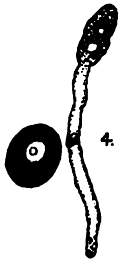
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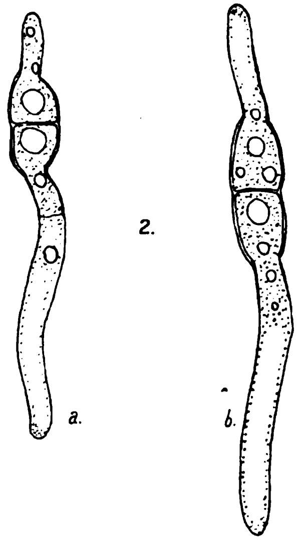
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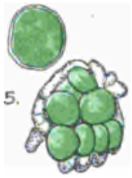
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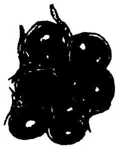
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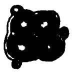
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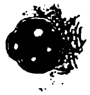
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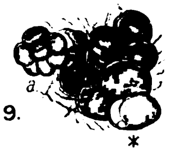
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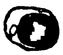
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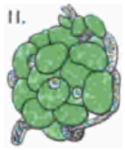
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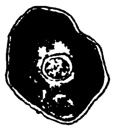
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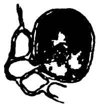
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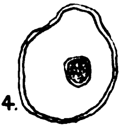
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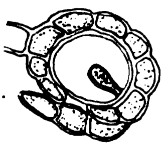
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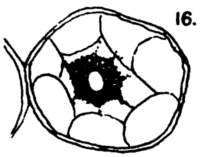
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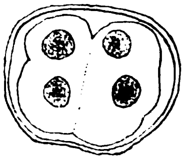
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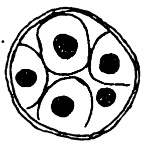
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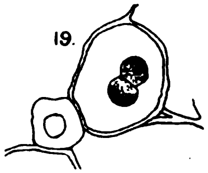
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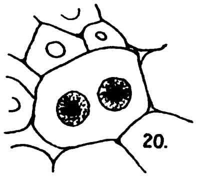
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CONTRIBUTIONS TO BIOLOGY
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XXI

Studies on the Flower and Embryo of Sparganium.

BY

DOUGLAS HOUGHTON CAMPBELL,
Professor of Botany, Leland Stanford Junior University.

[Reprinted from Proceedings of the California Academy of Sciences
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PALO ALTO, CALIFORNIA,
1899

PREFATORY NOTE.

This memoir is the twenty-first of a series designed to illustrate investigations and explorations connected with the Hopkins Seaside Laboratory, an adjunct of the biological laboratories of the Leland Stanford Junior University. These investigations have been carried on by means of the assistance given by Timothy Hopkins, Esq., of Menlo Park, California. This memoir appears in the publications of the California Academy of Sciences, the present edition being a reprint.

OLIVER P. JENKINS,
CHARLES H. GILBERT,
Directors Hopkins Laboratory.

Date of publication, July 21, 1899.

STUDIES ON THE FLOWER AND EMBRYO OF SPARGANIUM.

BY DOUGLAS HOUGHTON CAMPBELL,

Professor of Botany, Leland Stanford Junior University.

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THE genus *Sparganium* Tourn. includes about a dozen species distributed over the northern hemisphere, but also represented in New Zealand and Australia. The genus is a peculiar one, and there has been much diversity of opinion as to its affinities with other Monocotyledons. It has usually been associated with *Typha* in the family Typhaceæ, but the present view (Engler and Prantl, 1889) is that it should be considered the type of a separate family, Sparganiaceæ, with the Pandanaceæ or Screw-pines as its nearest allies.

The genus has not been extensively studied, but our knowledge of the development of the flower and embryo of the European *S. ramosum* is fairly complete (Hegelmaier, 1874; Dietz, 1887). The other species have, so far as I know, been treated from the standpoints of the descriptive botanist only, and no account of the embryo-sac has

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yet been published. Some years since I collected a small amount of material of the flowers of the common eastern species, *E. eurycarpum* Englm., and an examination of this material revealed several puzzling peculiarities of the embryo-sac, which were not clearly understood at the time. Figures of a few of these were published two years ago (Campbell, 1897), but lack of proper material, as well as other work, prevented any further study at the time. During the summer of 1896 a trip to Japan enabled me to procure a few specimens of the Japanese *S. longifolium* Turcz., and during the past season a good supply of *S. simplex* Huds. was collected in August at Tallac on Lake Tahoe. This species proved very satisfactory for study, and was made the principal subject of my investigations. In September, through the kindness of Miss Eastwood, a quantity of *S. Greenii* Morong. collected at Lake Merced, near San Francisco, was sent me, and served to supplement the work done on *S. simplex*. My material of the latter species was much more complete than that of any of the others, and moreover it proved easier to handle. The results obtained from a study of this species have been compared, so far as was possible, with those from the other species mentioned.

A preliminary statement in regard to *S. simplex* has already been published in a recent number of the "Botanical Gazette" (Campbell, 1899); but this refers simply to certain of the most striking points concerning the embryo-sac, and no account of the embryo is included.

Unfortunately all of the material collected was too old to show the earlier stages of development of the flower, so that the early history of the pollen and embryo-sac could not be traced. In the youngest flowers examined, the structures of the embryo-sac were already complete, and in most cases the embryo-sac was ready for fertilization. Hence in the present paper the study of the flower begins at the time when it is ready for pollination.

In the preparations of the material, various reagents were employed in fixing it: one-half to one per cent. chromic acid, saturated alcoholic solution of picric acid, saturated alcoholic corrosive sublimate, and weak Flemming's solution were employed, but of these the corrosive sublimate, on the whole, proved most satisfactory. The material was imbedded in paraffin and the sections were stained, usually with a double stain of Bismarck-brown and safranine, although in some cases they were stained *in toto* with alum-cochineal before they were imbedded.

I. THE FLOWER.

All of the species of *Sparganium* are monœcious, both staminate and pistillate flowers being aggregated in dense heads which are either sessile or borne on short pedicels. The lower heads are always pistillate and the upper ones staminate. The latter are usually much more numerous. In *S. simplex* and its allies the main axis is unbranched, while in the other species, e. g., *S. eurycarpum* and *S. Greenii*, the stem is branched.

Both sorts of flowers are exceedingly simple in structure. The individual flowers are borne in the axils of small bracts, and are themselves surrounded by a varying number of small membranous leaves which are usually considered to represent a very simple perianth. The male flower is composed of three or more stamens, while the female flower has either a single carpel, as in *S. simplex*, or a compound pistil composed of two completely united carpels, as in *S. ramosum* or *S. Greenii*.

The development of the flower has been studied to some extent in *S. ramosum* (Dietz, 1887), and is briefly as follows: Upon the primary axis are borne elevations which, in the lower part of the axis, where they are produced in axils of leaves, may develop into secondary axes, but in the upper portions of the axis, form at once the young inflorescences. In *S. simplex* and its allies, this axis does not branch, and all of the lateral axes develop into heads of flowers.

In *S. simplex* the lower three or four of these heads develop the pistillate flowers, while the number of staminate heads is usually larger.

The individual flowers, according to Dietz (l. c.), arise as small prominences upon the hemispherical fundament of the inflorescence, and upon these prominences arise secondary outgrowths which develop respectively into stamens or carpels. Dietz does not describe in detail the development of the stamen, and unfortunately my own material was too old to show this, so that it is not now possible to make a comparison with such Monocotyledons as have been investigated.

The scales of the perianth arise early, but Dietz does not describe their development.

To judge from his somewhat brief account and very diagrammatic figures, the development of the carpel and ovule is much like that of the low types like *Zannichellia* and *Lilæa*, which *Sparganium* resembles in these respects more than it does *Typha*, with which it has usually been associated. While further investigations are required before this can be decided, it looks as if in *Sparganium*, also, as in other low Monocotyledons, that the solitary ovule is of axial origin and not a product of the carpel.

The pistillate flower in *S. simplex* (fig. 1) consists of a single carpel surrounded by about six delicate membranaceous scales which form the perianth. Engler (Engler and Prantl, 1889) figures these in this species as having entire margins, but the form studied by me had the end of the narrowly spatulate scale sharply toothed (fig. 2), and the most recent figure (Britton and Brown, 1896) of this species shows the same thing, but with fewer teeth than my specimens. A delicate midrib traverses each scale. The ovary in this species merges gradually into the slender style which terminates in the narrowly sagittate stigma which is covered with minute papillæ.

In *S. longifolium*, which in many respects resembles *S. simplex*, the style and stigma are both shorter. In a second group represented by *S. Greenii* and *S. eurycarpum* the pistil is composed of two completely united carpels, and the resulting fruit is two-seeded. In both of these the style is very short or quite absent and the two stigmas are very long (fig. 4). The base of the ovary is also less tapering than in *S. simplex* and the perianth scales are heavier and nearly or quite entire at the apex.

S. simplex, which was the species principally studied by me, is a wide-spread form occurring throughout the northern hemisphere. In California it is confined to the higher mountains, the specimens collected by me being found near Lake Tahoe which has an elevation of over 6,000 feet above sea-level.

The Staminate Flower.

In *S. simplex* the staminate flowers form dense heads, each flower consisting of about six stamens. Just before the dehiscence of the anthers, the filaments elongate very much, so that the head becomes much looser, and the pollen is readily dislodged by the swaying of the slender filaments, much as in the grasses and sedges. The anther has four loculi as in most Angiosperms and offers no specially noteworthy peculiarities. The other species seem to agree closely in the structure of the stamen and were not critically examined.

The pollen-spores of *S. simplex* are small globular cells (fig. 6) and at maturity show the usual division of the nucleus into a larger vegetative one, and a smaller generative nucleus, but the latter was not seen to divide again while the pollen remained within the anther. Probably the final division of the generative nucleus takes place within the pollen-tube. Perhaps owing to its small size it was not possible to demonstrate the presence of a definite generative cell, the nucleus apparently lying free in the cytoplasm of the pollen-spore. As the cytoplasm of the ripe spore is very dense and stains strongly, it was not always easy, even in sections, to clearly distinguish the nuclei. The outer spore-membrane is marked with fine granulations but is not very thick. In this species there was almost always present in the ripe spore a structure which closely resembles the small vegetative prothallial cell in the germinating microspores of such heterosporous Pteridophytes as *Isoetes* and *Selaginella*. Chamberlain (1895) speaks of such a prothallial cell as an occasional occurrence in *Lilium Philadelphicum*, but except for this reference I am not aware of any reference to such a structure in the angiospermous pollen-spore. This prothallial cell, if such it is, in *Sparganium simplex* is lenticular in form (fig. 6), and separated from the body of the spore by a very well defined membrane which stains strongly with Bismarck-brown. While it was not possible to demonstrate positively the presence of a nucleus in this cell, there was usually to be seen a central body which stained more deeply than the rest of the cell with the usual nuclei stains and had much the aspect of a partially disorganized nucleus. While it seems very likely that this really represents a prothallial cell, homologous with the similar one in the microspores of *Isoetes*, for instance, its real nature cannot be positively assumed until its history has been followed.

The stamens of *S. Greenii* closely resemble those of *S. simplex*, but the pollen-grains did not show any trace of the prothallial cell, and the epispore is marked with fine reticulations. At one point (fig. 7) these were absent, and the clear area probably marks the point at which the pollen-tube emerges.

The Pistillate Flower.

The pistil may be composed of a single carpel, as in *S. simplex* and *S. longifolium*, or of two completely united ones, as in *S. Greenii* and *S. eurycarpum*. In *S. simplex* (fig. 3) a longitudinal section of the ovary shows the single anatropous ovule pendent from the upper part of the ovarian cavity. The narrow canal traversing the style opens into the ovary close to the base of the funiculus of the ovule.

The funiculus is rather slender and has a single axial vascular bundle. The nucellus is oval and there are two integuments usually found in the ovules of Monocotyledons.

The outer integument extends above the inner one and its upper margins are somewhat enlarged, so that the micropyle is quite closed.

II. THE EMBRYO-SAC.

The youngest embryo-sacs met with had the egg-apparatus and antipodal cells developed, and nothing can be stated as to their early history. As the ovule at the time of fertilization is of the ordinary type, it is not probable that there are any marked deviations from the type in its early development.

In *S. simplex* (figs. 3, 8) the mature embryo-sac is broadly oval in outline and is covered at the apex by about two layers of nucellar cells, the central ones somewhat elongated, so that the apex of the nucellus is slightly pointed. At the sides there are about four layers of cells in the nucellus, and these remain permanently and are not destroyed by the developing embryo-sac as so often happens. Within the embryo-sac the granular cytoplasm is principally confined to a thin parietal layer, except that surrounding the primary endosperm-nucleus there is a considerable amount of granular cytoplasm.

In *S. Greenii* (fig. 5) the two carpels are completely united. A section of the ovary shows a long central placenta formed by the coherent inner faces of the carpels, and from the upper part of the placenta depend the two ovules. These correspond in structure with those of *S. simplex* but are somewhat longer and more slender, although they are less constant in form than in that species. The embryo-sac is longer and narrower and more pointed at the ends. The part of the nucellus above the apex of the embryo-sac is thicker, there being usually about four layers of cells at this point.

Sparganium longifolium is much like *S. simplex* in the form of the pistil, except for the shorter style and small stigma. The ovule is of about the same size and shape, and the embryo-sac, so far as could be judged from the small amount of material available, closely resembles that of *S. simplex*, and as in that species there are but two, or at most three, layers of cells at the apex of the nucellus.

The common eastern *S. eurycarpum*, while resembling more nearly *S. Greenii*, differs from it in some details. The ovary is broader, due to an enlargement of the outer cells, and there are numerous enlarged cells present which contain bundles of rhaphides, or needle-shaped crystals, presumably of calcium oxalate. These spicular cells also occur in the placenta, and while not entirely absent from the ovary of *S. Greenii* are much less abundant. There are also found on the upper surface of the placenta papillate cells which are much less marked in *S. Greenii*. These are doubtless connected with the conduction of the pollen-tubes. The structure of the ovule itself, and the embryo-sac are much alike in the two species.

In all the species examined the cells of the nucellus persist, and the subsequent enlargement of the upper part of the integuments and the apex of the nucellus gives rise to the peculiar cap ("Samen-deckel" of Hegelmaier) which characterizes the ripe seed of all species of *Sparganium*.

The broadly oval embryo-sac of *S. simplex* is scarcely at all narrowed at either end. In all specimens examined the two polar nuclei had already completely fused, and it is evident that the fusion of them to form the primary endosperm-nucleus occurs some time before the fertilization of the egg-cell. The large endosperm-nucleus (fig. 10) is imbedded in a considerable mass of granular cytoplasm which is elsewhere confined to the thin parietal layer. The position of the endosperm-nucleus is not constant, and it was found in nearly all positions in the sac; sometimes it lay close to the egg-apparatus, sometimes it was near the antipodal cells.

The egg-apparatus is of the normal structure, and compared to the size of the embryo-sac is small. A good deal of variation in the size of the egg and synergidæ was noted, and these differences did not appear to be necessarily connected with the age of the egg-apparatus. The egg-cell was sometimes in the same plane as the synergidæ (fig. 8), and sometimes it was lower down and a good deal elongated (fig. 11). In either case it was nearly hyaline, with only a relatively small amount of granular contents surrounding the nucleus which is usually placed near the free end of the ovum, i. e., the end which projects into the embryo-sac (figs. 8, 11). The synergidæ are alike, somewhat smaller than the egg and filled with densely granular cytoplasm in which lies the small nucleus. All the nuclei of the egg-apparatus have a very distinct nucleolus which is especially conspicuous in material stained with anilin-safranine. The rest of the nucleus, however, does not stain strongly with this reagent, the nuclei preliminary to fertilization appear to have very little chromatin. The nucleus of the egg is somewhat larger than the synergidal nuclei but otherwise closely resembles them.

Above the synergidæ there was seen in many specimens what looked like the remains of the tapetal cells (fig. 8). This mass stained strongly with Bismarck-brown but showed little structure and probably represented the disorganized remnants of one or more tapetal cells. As the younger stages were lacking in my preparations the origin of this body can only be conjectured.

In none of the specimens of *S. simplex* were the separate polar nuclei observed. The large endosperm-nucleus resulting from their fusion is, however, conspicuous. It is much larger than the other nuclei of the embryo-sac, and has a very large nucleolus (figs. 10, 11).

The antipodal end of the sac in this species is almost flat, although there may be a slight depression where the antipodal cells are found. The early history of the latter could not be followed, as the material was all too old; but at the time the egg is mature, these cells are remarkable for their very small size, which is in striking contrast to their later development. Not infrequently where these cells had collapsed in the process of embedding, they could not certainly be distinguished, and may very easily be overlooked. There was nothing, however, to indicate that they are ever really absent. Where they are uninjured (fig. 12) they may usually be seen to be arranged in the same plane and are very shallow, projecting only very slightly into the cavity of the embryo-sac. The cytoplasm of these cells is finely granular but does not readily stain at this stage. The nuclei are very small and inconspicuous, and it is sometimes difficult to demonstrate them at all. In no case did they stain readily with the usual reagents.

In *S. Greenii* the appearance of the antipodal cells is somewhat different and this resembles more those of other Monocotyledons (fig. 21). The base of the embryo-sac is here prolonged into a narrow cavity within which lie the antipodal cells. These are not usually in the same plane, but one of them lies above the other two, to which it bears much the same relation that the egg-cell does to the synergidæ. The antipodal cells in this species are much larger than in *S. simplex*, and the cell contents denser, and the nuclei are larger and readily demonstrated, as they stain without difficulty.

So far as my observations go upon *S. longifolium* and *S. eurycarpum*, they are more like *S. Greenii* than *S. simplex* in the form of the antipodals, although *S. longifolium* is to some extent intermediate in character.

III. FERTILIZATION.

The small size of the pollen-spore and nuclei is not favorable to a study of the details of fertilization, and although in several instances the pollen-tube was detected within the embryo-sac, nothing was observed which indicated that the fertilization was in any way different from that of other Angiosperms. The pollen-tube after reaching the micropyle pushes down between the cells of the nucellus, which are not injured by its passage. On entering the embryo-sac, it apparently comes into close contact with one synergid, which is probably destroyed in most cases, although this is not necessarily the case, as in one instance, at least, the end of the pollen-tube was seen within the embryo-sac, although both synergidæ were still intact. The very small size of the generative nucleus makes it extremely difficult to detect, and only a few incomplete observations were made on its behavior after entering the sac. In one case (fig. 9) a small, deeply stained body was observed within one of the synergidæ, and this very probably was one of the generative nuclei on its way to the egg-cell. In another instance (fig. 13) there was visible within the egg a small body looking like a nucleus, but not staining as deeply as might have been expected of the male pronucleus. In the same preparation (fig. 14) there was a small granular mass attached to the end of the pollen-tube, and looking as if it might have been discharged from it into the cavity of the embryo-sac, but there was nothing to indicate the discharge of the second generative nucleus and its fusion with the endosperm-nucleus as described by Nawaschin; however, my observations were too incomplete to warrant any positive statement on this point. One of the synergidæ can usually be detected for a long time after fertilization has been effected, as has been observed in so many other cases.

After fertilization has been effected the egg-cell enlarges very little, and after the membrane is developed about it, it remains unchanged for a long time. At this time the unicellular embryo (fig. 24) is a more or less pear-shaped cell, sometimes in contact with the upper wall of the embryo-sac merely by a very small part of the pointed lower end, sometimes having a much broader base of attachment. In this condition it remains until the sac has increased a good deal in size and the development of the endosperm is well advanced. Owing to this slow development of the embryo the earlier stages between the unicellular condition and that shown in fig. 37 were missed.

IV. THE SECONDARY GROWTH OF THE ANTIPODAL CELLS.

While the embryo-cell remains unchanged for a long time, the other structures of the embryo-sac undergo marked changes. Almost the first visible result of fertilization is a marked increase in the size of the antipodal cells. In

S. simplex where this was especially studied, and of which a preliminary account has already been published (Campbell, 1899), this is especially noteworthy. Before fertilization (fig. 12) the antipodal cells are extremely inconspicuous, but almost immediately after fertilization has been effected they rapidly increase in bulk, and at the same time show other marked evidences of active growth. The cytoplasm becomes more coarsely and densely granular, and the nuclei enlarge to several times their original size and at the same time take up stains much more readily than before (fig. 26). As the antipodals increase in size they project strongly into the cavity of the embryo-sac and form a conspicuous nearly hemispherical body. The three original cells now rapidly divide until finally a very large mass of cells (fig. 30) results, probably larger than in any other Monocotyledon. The number of antipodal cells may finally exceed 150, a number greater than that yet recorded for any other Angiosperm.

In position and general appearance the group of antipodal cells most nearly recalls that of many Gramineæ (Hofmeister, 1861; Fischer, 1880, etc.). An important difference is that in the latter the development of the antipodal complex is completed previous to the fertilization of the egg. The method of its development, however, is very similar in the two cases.

The embryo-sac in those grasses which have numerous antipodal cells has at first the ordinary number, three, and these subsequently divide to form the larger number ultimately developed. Hofmeister (1861) states that in the Triticeæ the number may be 6–12 and Körnicke (1896) found 36 or more, a large number, but very much less than the normal number finally developed in *Sparganium simplex*.

The first division of the nuclei of the antipodal cells occurs shortly after the first division of the primary endosperm-nucleus. Following the first division, the increase in size of the antipodal cells and the divisions proceed rapidly, while the endosperm at this stage remains slightly developed. There seems little question, that as Westermaier (1890) pointed out in the grasses, these enlarged antipodal cells replace physiologically for the time being the endosperm, and elaborate food materials for the growth of the developing embryo-sac and embryo.

The first divisions in both endosperm and antipodal cells take place before there has been any marked increase in the size of the embryo-sac; but later there is a rapid increase in the size of the ovule, which probably coincides with the first divisions in the embryo.

Körnicke (1896) in his studies on the antipodal cells of various Gramineæ was unable to detect any karyokinetic figures in these and was inclined to think that the divisions of the nuclei might be direct. This view appeared to be hardly likely, as the nuclei in the developing antipodal cell of *Sparganium* appeared entirely normal, and the cells were actively growing and dividing, not a condition in which one would look for direct nuclear division. Fortunately a preparation was finally secured in which some of the antipodal nuclei were actually in process of division (fig. 29), and it was seen that the division is the typical karyokinesis, which it is safe to say is the normal type of nuclear division, at least in the early stages. In the case under consideration the endosperm-nuclei were also dividing.

In most cases, possibly always, the first division of the nucleus in the antipodal cells in *S. simplex* is not accompanied by the formation of a division-wall, and the enlarged antipodal cells show plainly two conspicuous nuclei (fig. 29). Later, however, all the nuclei become separated by walls and each of the very numerous antipodal cells has evidently but a single nucleus (fig. 30). In some older ones, however, two nuclei were sometimes seen, so that it would seem that the last nuclear division, like the first one, may be independent of cell division. There is thus a certain analogy with the behavior of the normal endosperm-cells which would indicate that the antipodal cells are not markedly different in nature from the endosperm-cells, and may be really homologous with these.

The densely granular cytoplasm of the antipodal cells does not fill them uniformly, but there are usually present large vacuoles (fig. 28). The first division-walls in the antipodals of *S. simplex* are vertical, so that the mass has the form of a disc, but later transverse and oblique divisions may also occur, although the majority of the walls are vertical and the cells become a good deal elongated (fig. 30).

As the seed grows older the antipodal cells begin to show signs of disintegration, but in no cases where sections were made had they entirely disappeared, and traces of them probably persist even in the ripe seed.

The earlier stages of the antipodals were studied also in *S. Greenii* and *S. eurycarpum*, but material was not available for the later development which is probably not entirely like that in *S. simplex*. In *S. Greenii* the antipodals at the time the egg is fertilized are, as we have seen, much more conspicuous than in *S. simplex*. They are also differently arranged, not usually lying in the same plane, but one of them being above the other two (fig. 33). In one instance (fig. 16) there was present above the three antipodal cells a large cell which looked like a fourth antipodal, but as this was the only case seen, there was no clue as to its origin. Otherwise the embryo-sac appeared to be entirely normal. In this species (*S. Greenii)* the polar nuclei remained separate, although often in close contact (fig. 20) until after the fertilization of the egg, and in this respect it differs from *S. simplex* and probably from *S. eurycarpum*. There is also much greater variation in the size of the embryo-sac in *S. Greenii* than in *S. simplex*. As a rule the egg and synergidæ are larger also than in *S. simplex* and sometimes the former show a reticulate appearance in the cytoplasm, due to the presence of numerous vacuoles (fig. 18), an appearance which was not seen in the specimens of the latter species. The embryo-sac in *S. Greenii* is relatively narrower than in *S. simplex,* and there are three or four layers of cells at the apex of the nucellus, which is also larger than in that species. As we have already stated, the antipodal cells, before the fertilization of the egg, are noticeably larger than in *S. simplex*, and two are placed below the third one, and lie in the depression at the base of the embryo-sac. This is much narrowed, and may account for the fact that sometimes these two lower antipodal cells take no part in the formation of the group of antipodals formed after fertilization (fig. 36). In such cases they remain for a long time quite unchanged, and ultimately show signs of disorganization. The upper of the three original cells, however, enlarges greatly and assumes a vesicular form, projecting strongly into the cavity of the embryo-sac. The nucleus of this cell, as in the older antipodal cells of *S. simplex*, enlarges very much, soon undergoes division, and this is quickly repeated, so that four cells, arranged quadrant-wise, result. Where this was the case division-walls could be seen between the nuclei. Sometimes, however, the lower antipodal cells also enlarge (fig. 35) and the development proceeds much as in *S. simplex*, except for the relative positions of the cells. How far the antipodal cells may finally develop in *S. Greenii* could not be ascertained, as the next stages were absent from my material. So far as could be judged from the few stages examined, the cells show a tendency to become more inflated than in *S. simplex* and the granular contents are less abundant, but these peculiarities, which seem also to characterize *S. eurycarpum*, may not be constant, and a study of the later stages in these species will be necessary before the question can be definitely decided.

V. THE EMBRYO.

The development of the embryo does not, at first, keep pace with the development of the antipodal cells and endosperm, and for some time it remains without any apparent change in appearance. Although a large number of sections were made, it was impossible to find stages between the unicellular embryo and such advanced stages as that shown in fig. 37. It is therefore impossible at present to compare the first divisions in the embryo of *S. simplex* with the corresponding stages of that in *S. ramosum*, the only species hitherto examined. As the later stages agree quite closely in the two species, it is not likely that there are any very marked differences in the early stages. Nevertheless, it is much to be regretted that these early stages could not have been compared, and it is to be hoped that these may be examined soon in our American species.

According to Hegelmaier (1874) the embryo cell in *S. ramosum* divides into three superimposed cells, but it is not clear whether the second division is in the upper or lower of the two primary cells. Before any longitudinal divisions are formed there may be one or two more transverse divisions, making thus a single row of four or five primary segments in the embryo. A very similar account is given by Nörner (1881) for the young embryo of several grasses, except that he criticizes Hegelmaier's statement as to the time of the fourth and fifth transverse walls, claiming that these are probably not formed until after the first longitudinal divisions. He concludes that three is the regular number of the primary segments in most Monocotyledons. The more recent investigations in the embryo of the lower Monocotyledons (Schaffner, 1896; Chamberlain, 1895; Campbell, 1897, 1898, etc.) indicate that the basal cell, where this becomes enlarged, does not divide further, and that all the further transverse segmentation is in the terminal cells, but it is probable that in *Sparganium* the segments are the product of the division of the original basal cell.

So far as could be judged from an examination of the somewhat advanced embryo of *S. simplex* (figs. 37, 38, 39), it looked as if the first longitudinal divisions in the terminal segment occurred earlier than Hegelmaier gives for *S. ramosum*, and it is doubtful whether here there are more than three primary segments. A comparison of these stages with Hegelmaier's figures 5 and 13 indicated that possibly his segment 2 really belongs to the terminal segment.

The basal segment never becomes enlarged as it does in so many Monocotyledons, but remains usually very small and generally divides early by longitudinal walls into three or four cells, but sometimes a cross-section shows but two cells. The absence of the large vesicular suspensor cell found in *Naias*, *Alisma* and other Monocotyledons is largely a physiological phenomenon, doubtless connected with the nutrition of the developing embryo, and is intimately associated with the degree of development of the endosperm. Hegelmaier (1874) found that in *S. ramosum* the terminal segment gave origin to all the structures of the embryo except a portion of the root-apex. As he worked entirely with embryos which were simply rendered transparent, but not actually sectioned, he was unable to make out successfully all the details of the arrangement of the tissues in the older embryos. Nevertheless, his results, on the whole, were remarkable accurate, and show a close correspondence to my own preparations of *S. simplex* which were obtained from actual sections. He found that the cotyledon and stem-apex are both products of the terminal segment, and that the plerome of the root is also derived from this segment, and terminates at the wall separating segments I and II.

My own studies of the embryo were necessarily confined almost exclusively to *S. simplex*, as the material collected of the other species did not contain the proper stages of the young seed. The youngest embryos obtained are shown in figs. 37–40. While these agree in general with Hegelmaier's figures of similar stages in *S. ramosum*, there are certain differences which may be noted. The basal, or primary transverse wall (*x*) which corresponds probably to his wall (*i*), is regularly lower down than his figures, indicating that the terminal cell of the young embryo is from the first larger than in *S. ramosum*. It is possible that his segment II may be included in the portion above the basal wall, but this is not probable, as evidences of median vertical walls extending from the apex of the embryo to the basal wall can generally be made out, and from a study of the older stages it is evident that the plerome of the root extends quite to the basal wall, as Hegelmaier describes for *S. ramosum*. The hypobasal portion of the embryo narrows rapidly, and this portion shows ordinarily but two transverse segments, instead of the three or four found in *S. ramosum.* The small basal segment, which is in contact with the apex of the embryo-sac, varies a good deal in size, this being correlated with the form of the original embryo-cell. If this tapers much, so as to have a small point of attachment, the basal segment remains very small and pointed (fig. 42), but if the embryo-cell is flattened where it is in contact with the wall of the embryo-sac, the basal segment of the embryo is correspondingly broader and shows more divisions.

A median section of such an embryo shows the limits of the three primary segments still visible (fig. 38). This terminal segment is very much larger than the others, and, as already stated, relatively larger than in *S. ramosum.* The first divisions in all the segments are median vertical ones, and it is clear from studies of transverse sections that there are normally intersecting median walls which divide each segment into four equal quadrants. The divisions are less constant in the basal segment, especially when it is small, and transverse sections of this often show only two or three cells, one or both of the second median walls being suppressed. The next divisions are usually vertical also, but there is evidently no absolute rule as to their arrangement. In fig. 40 is shown a series of cross-sections of a young embryo, and it is clear that the divisions are not always entirely alike in the different quadrants of the same section (see fig. 44, *b*). Probably, in most cases, the first division-wall formed in the quadrant is curved, and extends from the quadrant-wall to the periphery. This is then followed by a series of periclinals which cut off the epidermis. Sometimes, however, it looks as if the first walls were periclinals, thus determining at once the separation of the epidermal layer. Hegelmaier shows much the same variation in *S. ramosum* (e. g. his figures 6 and 8).

The variations in the basal segment have already been referred to. It may divide into equal quadrants (fig. 44, *a*), but more commonly there is a suppression of one or both of the second quadrant walls. Where the basal segment is unusually large, transverse or oblique divisions may also occur (fig. 39). A transverse section of the second segment at this stage shows eight peripheral cells surrounding four central ones.

In the upper segment, the next divisions are transverse, and sometimes this gives the appearance of a complete transverse division across, and it is possible that the segment numbered II by Hegelmaier may in some of his figures really refer to a secondary transverse division in the terminal segment. The separation of the epidermis is brought about as in the second segment, and soon after another series of similar divisions separates the central group of plerome cells from the periblem. The plerome extends to the basal wall where it ends abruptly, not being found at all in the two lower segments. In cross-section (fig. 44, *c*) the young plerome shows four cells, one belonging to each quadrant, but there are soon found other longitudinal walls which increase the number of plerome cells.

The older embryo is not perfectly cylindrical in form, but is somewhat broader in the plane of the future cotyledon. Sections made in this direction have the upper segment nearly circular in outline, but the median wall is often somewhat oblique, so that the segment is not always perfectly symmetrical. In this view the small basal segment usually shows a vertical division into two nearly equal cells. In the cotyledon, which constitutes the major part of the terminal segment, the epidermis is already clearly differentiated, but this is not always so evident in the second segment, where the interlayer of cells usually undergoes another periclinal division, which is never the case, so far as I could determine, in the epidermis of the cotyledon. If the section is made at right angles to the face of the cotyledon (fig. 42) the embryo appears more pear-shaped in outline, and the basal segment may appear undivided. Cross-sections of similar embryos show that in such cases the basal segment is composed of but two or three cells. In a number of instances the second transverse wall was very oblique (fig. 42) and might even intersect the basal wall, and such embryos resemble very much the embryo of such grasses as *Triticum* and *Hordeum*, figured by Nörner (1881). Hegelmaier does not show these oblique walls in his figures of *S. ramosum*, and in this respect *S. simplex* is more like the grasses than is *S. ramosum*.

The primary tissues are now pretty well defined. The central plerome-strand extends to the basal wall and is separated from the epidermis by one layer of periblem cells (fig. 46). In the segment below, the superficial cells, as we have seen, divide again by periclinal walls, so that there are often two well defined layers of cells, evidently derived from a periclinal division of the primary epidermis. In the basal segment there are seldom more than four cells, and in case there is another segment between the basal one and the second segment (fig. 51) its divisions are quite irregular.

Hegelmaier's account of the origin of the different members of the embryo in *S. ramosum* corresponds closely to what was seen in *S. simplex*. Much the greater part of the embryo is taken up by the cotyledon which elongates rapidly, so that the embryo soon becomes several times longer than broad, this growth in length being mainly in the cotyledon, the stem and root remaining short. The stem-apex originates from the terminal segment, but on one side well toward the base. Its position and origin correspond closely to those in the grass-embryo, to judge from Nörner's account and figures (Nörner, 1881). In its origin from the terminal segment it differs from such Monocotyledons as *Alisma* and *Naias*, where the stem-apex belongs to the second segment. *Zannichellia*, however, has a terminal stem-apex, and Solms-Laubach (1878) describes several Monocotyledons with terminal stem-apices. In *Lilæa* (Campbell, 1898) the stem-apex is probably derived from the terminal segment as in *Sparganium*. *Sparganium* is, therefore, in regard to the origin of the stem-apex, intermediate between such extreme forms as *Zannichellia* and the majority of Monocotyledons investigated, in which the stem-apex arises from the second segment.

Cross-sections of the older embryo are usually more or less oval in outline, the longer axis coinciding with the face of the cotyledon. In sections made just above the basal wall (fig. 47), the first indication of the stem-apex (*st*) is evident in a more rapid division in the epidermis where the cells are decidedly narrower. At this time, the section of the plerome shows about nine cells, and the original quadrant divisions are very evident. The stem-apex appears to be the product of one only of the quadrants, and soon becomes sunk in a depression formed by the excessive growth of the basal cells of the cotyledon immediately adjacent to it (fig. 44). The stem-apex later becomes deeply sunk in the narrow cavity formed by the excessive growth of the base of the cotyledon, and this forms a sheath, such as is so frequently met with among the lower Monocotyledons (figs. 49 and 53).

The plerome-strand is continued upward into the cotyledon and downward into the root, but there is no trace of a cauline bundle. The other tissues of the root arise from the cells of the second segment of the embryo. This also divides at first by quadrant walls, and later a central growth of four cells (fig. 44, *b*) is separated from an outer row of cells. The latter again divides into two by periclinal walls. The initial group of cells, which contributes to the growth of the periblem, dermatogen and calyptrogen, is derived from the four central cells which may be said to constitute the initial for all the tissues of the root except the central plerome-cylinder.

Before the embryo is mature, the second leaf makes its appearance on the side of the stem opposite the cotyledon. The nearly flat stem-apex develops a protuberance on its outer side, and this quickly assumes the form of a short cylindrical body whose tissues are continuous with those of the stem, except that the plerome-cylinder connects with that of the root.

The embryo rapidly increases in size as the seed ripens, and finally occupies the whole axial part of the embryo-sac. The space between it and the wall of the sac has in the meantime become completely filled with the endosperm. The full-grown embryo (fig. 52) is a spindle-shaped body, of which the cotyledon constitutes much the greater portion. The outer edges of the sheath at the base of the cotyledon overlap so as to completely conceal the stem-apex and second leaf (fig. 54).

A longitudinal section through the base of the full-grown embryo (fig. 53) shows that the root is very broad and short. Occupying its axis is the conical plerome which in section shows about six rows of cells; this ends at the basal wall whose limits are still discernible. No single initial cell could be made out at the apex of the plerome, nor could any absolute regularity in the segmentation of the terminal cells be recognized. Connected with the main plerome-strand are smaller branches extending into the young leaves, but, as already stated, none is given off to the stem. Between the plerome of the root and the epidermis there are five or six layers of cells.

The origin of the other tissues of the root can be traced back to the central group of cells lying next the apex of the plerome and derived from the central cells of the second segment of the embryo. There are probably four of these initial cells, and two can usually be seen in longitudinal sections. Periclinal segments are cut off from those which add to the root-cap, and lateral segments are also formed which, dividing again, form the initials for the dermatogen and periblem. The primary root of the embryo of *Sparganium* therefore conforms closely to the type described by De Bary (1884), as found most commonly in Monocotyledons. The root-cap is well developed in the older embryo and has the form of a biconvex lens, as the central part of the root-apex is strongly concave.

A noticeable difference between the embryo of *Sparganium* and that of most other aquatic Monocotyledons hitherto examined, e. g. *Alisma*, *Naias*, *Lilæa*, etc., is the absence of the larger vesicular suspensor cell, so conspicuous in those forms. This cell is evidently of great importance in these plants, and directly concerned with the food supply of the young embryo. Its absence in *Sparganium*, the Gramineæ, and such Aroids as have been examined is no doubt to be sought in the better development of the endosperm in these forms, and possibly also in the presence of numerous antipodal cells, which assume temporarily the functions of the endosperm.

The first division of the primary endosperm-nucleus occurs almost immediately after fertilization. At this time the endosperm-nucleus is, usually at least, near the antipodal end of the sac. The divisions are repeated until there are formed in the usual manner many free nuclei arranged in a single layer in the parietal cytoplasm (fig. 30). These nuclei are more or less flattened and possess a single large nucleolus. At the apex of the sac they are more numerous, and the cytoplasm is more abundant and quite surrounds the young embryo. As usual, the first cell-division in the endosperm takes place at the apex and proceeds toward the antipodal region.

While the endosperm-nuclei have been dividing, and the peripheral layer of protoplasm is still very thin, the antipodals have increased enormously in bulk and divided rapidly to form the large mass of cells found at the antipodal end of the sac. We have already spoken of the karyokinetic division of the antipodal nuclei and it is very doubtful whether even in the binucleate cells sometimes found in the later stages this division is ever direct, as it has been found to be in the enlarged antipodal cells of a number of plants (e. g. in Ranunculaceæ, Mottier, 1895). As the embryo-sac enlarges it changes its form somewhat in *S. simplex*, becoming relatively much narrower at the upper end which early becomes completely filled with endosperm (fig. 37).

In the micropylar end of the sac the protoplasm early becomes much denser, the nuclei are larger than at the sides of the sac and not confined to a single layer. The nuclei increase a good deal in size before the cell-walls are formed between them (fig. 57).

As *Sparganium simplex* shows very clearly the endosperm formation, this was studied in some detail. Before the division-walls are evident, the nuclei are arranged at nearly equal distances. The delicate radiating lines connecting them are clearly evident (fig. 57), and in these the cell-plates are soon visible, and the nuclei are thus enclosed in polygonal areas which become cells by this transformation of the cell-plates into cellulose membranes (fig. 58). The cells at the apex of the sac are quite irregular in form and completely surround the embryo (fig. 37). At the sides of the sac these cells seen from the surface are often regularly hexagonal. The endosperm-cells at the apex have much denser contents than those at the sides, which are almost transparent. Figure 56 illustrates the way in which the development of the endosperm proceeds centripetally. This section is a nearly median one and shows how the nuclear divisions are mainly in a plane parallel to the periphery of the sac. The first-formed endosperm-cells are at first open on their inner face, and when the nucleus divides a division-wall is found closing up the outer cell, but leaving the inner one also open. This continues, one layer of new cells after another being added to the endosperm, until finally the whole upper part of the sac is filled up, but the lower portion remains open in the center up to a late enlarged period. Free nuclei can always be seen in this open part of the sac, lying in the layer of protoplasm covering the free walls of the inner endosperm-cells.

The endosperm-nuclei become a good deal enlarged before the division-walls are formed, and these enlarged nuclei generally show several nucleoli. The younger stages have only a single nucleolus and the outline of the nucleus is round and oval. As they increase in size, it was found that the nucleolus became elongated and constricted (fig. 58), finally resulting in a division into two, generally unequal, portions. This is probably repeated in the case of those which have more than two nucleoli. Each nucleolus is surrounded by a clear area, while the rest of the nucleus presents a granular appearance. As the nucleus itself becomes more or less distorted in outline with the division of the nucleolus, and often appears lobed, it was at first supposed that we had to do with a case of nuclear fusion, but in reality it is more nearly a case of fragmentation. Hegelmaier (1885) figures a number of similar cases, and they have been often observed, but so far as I know the origin of the secondary nucleoli has not been studied.

As the seed ripens, numerous very large crystalloids are formed, at least in *S. simplex*, in the endosperm-cells surrounding the embryo (figs. 63, 64). These are beautifully fixed by the action of alcoholic corrosive-sublimate, and stain readily with anilin-safranine. They vary in shape, the most perfect ones being rhombic in outline. Often they were aggregated in large masses, but usually it was evident that these masses were composed of separate crystals. *Sparganium simplex* may be recommended as an admirable subject for demonstrating these bodies. The material collected of the other species was either too young or had not been treated with the proper reagents, so that I cannot speak as to the occurrence of these crystalloids in the endosperm of the other species. They have, however, been noted in *S. ramosum* Sachs (1887).

No hard testa is formed about the seed of *Sparganium*, although this outer part of the nucellus and the integuments persist until a late stage, and probably permanently. Engler's statement (1889) that the endosperm is only separated from the pericarp by the integuments needs confirmation. In the oldest stages examined by me, there were several layers of nucellus cells still evident. The development of the hard inner pericarp is readily followed. The cells early have thickening layers deposited upon their walls, and these later become very thick and have deep pits developed in them. This sclerenchyma is rather better developed in *S. Greenii* than in *S. simplex*, and sometimes in the former the thickening is so great as to almost obliterate the lumen of the cell.

Hegelmaier (1874) has studied in *S. ramosum* the development of the curious structure to which he applies the name "Samen-deckel." The structure of this in *S. simplex* agrees closely with his account. It is formed from an enlargement of the micropylar part of the integuments, which become very much swollen, and form two caps, one above the other. The upper part of the nucellus is also included, but the cap is principally derived from the integuments (fig. 59). The margins of the inner integument are prolonged upward into a conical beak which fits closely into the opening in the outer integument. The whole structure is enclosed in the space at the top of the ovary which remains as a conical cavity in the pericarp.

The fruit of *Sparganium* is not very unlike the caryopsis of the grasses, but differs in the persistence of the integuments and probably also of a portion of the nucellus. By a further compression and disorganization of these a typical caryopsis would be formed.

VI. ABNORMAL EMBRYO-SACS.

In *Sparganium*, as in most other low Monocotyledons hitherto examined, there are occasional deviations from the normal development in the embryo-sac. Some of these have already been noted by the writer (Campbell, 1897) in the case of *S. eurycarpum;* indeed, it was these abnormalities which directed attention to *Sparganium*. In both *S. simplex* and *S. Greenii* similar deviations from the type were noted.

The most usual form is a multiplication of the nuclei within the embryo-sac without any noticeable increase in its size. As in such cases (fig. 68) the embryo cannot be detected, and the egg-apparatus has either not been formed, or has disappeared, the most probable explanation is that the sac had not been fertilized, but that the vegetative tissue of the gametophyte, i. e., the antipodal cells and the endosperm, are capable of a limited growth. This is quite comprehensible if *Sparganium* is, as it seems to be, a very low type of Angiosperm, and the case might be very well compared to the limited growth of the prothallium in the heterosporous Pteridophytes when fertilization is not effected.

Other abnormal embryo-sacs are shown in figs. 65 and 69. In the first case, taken from an ovule of *S. simplex*, the embryo-sac was very broad and divided longitudinally by a membrane—whether of cellulose or not was not determined. Three antipodal cells having the appearance of the normal ones in a recently fertilized sac could be distinguished. The structures at the micropylar end of the sac were not clearly distinguishable. The extremely broad form of the sac suggested the possibility of there having been two embryo-sacs formed in the ovule, but if this was the case, they had become entirely confluent.

Another puzzling form in *S. Greenii* is shown in fig. 69. Here the antipodal cells were apparently normal, but the polar nuclei, which were in close contact, were separated from the cavity of the embryo-sac by an evident membrane, and the upper portion of the sac was similarly shut off. Occupying the extreme upper part of this was a body looking like a very large nucleus, but the nucleolus (?) did not appear homogeneous, and it is possible that this apparent nucleus was really a cell, as the nucleolus-like body was quite similar in size and appearance to the nuclei of the surrounding nucellar cells. No other nuclei could be certainly made out in this region, except a deeply staining small body close to the wall of a vesicle which lay below the large apical nucleus. If the latter is really a nucleus it probably means that one nuclear division in the upper part of the young embryo-sac had been suppressed, and no egg-apparatus developed.

In another specimen of *S. Greenii* the embryo-sac was seen to be completely filled with granular cytoplasm, and a similar condition has also been seen in *S. eurycarpum*.

VII. RECAPITULATION.

1. The stamen in *Sparganium* is of the usual type: the ripe pollen-spore shows but one generative nucleus, but in *S. simplex* there is regularly a structure present which probably represents a vegetative or prothallial cell which was not observed, however, in *S. Greenii*.

2. The early development of the embryo-sac follows the normal course; the egg-apparatus is small in *S. simplex* and the polar nuclei fuse completely before the egg is

fertilized; in *S. Greenii* they remain separate until after fertilization.

3. The antipodal cells are three in number and in *S. simplex* are very inconspicuous; after fertilization there is a remarkable secondary growth in the antipodal cells, resulting finally in a large cell-mass, containing in *S. simplex* over 150 cells.

4. The process of fertilization, so far as it was studied, offered no anomalies.

5. The development of the embryo in *S. simplex* agrees closely with that of *S. ramosum*, studied by Hegelmaier. There are regularly three primary transverse segments, of which the terminal one gives rise to cotyledon, stem-apex, and part of the root. The suspensor remains undeveloped, and in this respect the embryo is like that of the Gramineæ. The slight development of the suspensor is associated with the complete investment of the young embryo by the endosperm.

6. The stem-apex is lateral in origin like that of most Monocotyledons, but is not developed from the middle of the three primary segments.

7. The primary tissues of the embryo are very early developed, especially in the terminal embryonal segment. The plerome of the root is derived entirely from the terminal segment; the initials for the other tissues of the root arise from the middle segment.

8. The development of the endosperm follows the usual course, but is rather late in forming the first division-walls. The enlarged antipodal cells doubtless function at first as endosperm.

9. The large endosperm-nuclei have often several nucleoli which are formed by a fragmentation of the original nucleolus.

10. Large crystalloids are abundantly developed in the older endosperm-cells of *S. simplex*.

11. The inner pericarp develops into sclerenchyma with thick, deeply pitted walls. The development of the "Samen-deckel" is the same as described by Hegelmaier for *S. ramosum*.

VIII. THE AFFINITIES OF SPARGANIUM.

The genus *Sparganium* has until recently been associated with *Typha* in the family Typhaceæ, but Engler (1889) has pointed out that the differences between *Typha* and *Sparganium* are so great as to make such a union unwarranted, and he proposes placing *Sparganium* in a separate family, following the Pandanaceæ. Until more is known about the development of the Pandanaceæ, however, it will be impossible to decide how closely the two families are related. A thorough study of some species of *Pandanus* would be of great value in solving this question.

Hegelmaier (1874) has referred to certain resemblances in the embryo of *Sparganium* to that of the Gramineæ, and my own study of *S. simplex* confirms this. The extraordinary character of the antipodal cells also is strongly suggestive of the grasses. The probably terminal origin of the single ovule is also like that of the grasses, and this it also shares with most other low Monocotyledons. Indeed the solitary uni-ovulate carpel is probably the most primitive type among the Monocotyledons, and is not the result of a reduction. In this particular *S. simplex* is probably more primitive than the forms like *S. Greenii* and *S. eurycarpum*, in which the ovary is compound.

The type of fruit in *Sparganium* is not unlike that of the Gramineæ. While the majority of the latter have a caryopsis, there are others in which the fruit is nut-like, corresponding to that of *Sparganium* (see Hackel, 1890). A comparison of some of these forms with *Sparganium* would be interesting.

The monœcious flowers of *Sparganium* also are shared by some grasses, e. g. *Zea*, so that the possibility of an actual relation between these two puzzling families may very well be considered. Of course the resemblances may be purely fortuitous, but it is more likely that they indicate a real, even if remote, affinity, and any further study of the flower and fruit of the Gramineæ should consider this. In short, so far as a comparative study has been made, *Sparganium* shows a closer affinity with the Gramineæ than with any other family, unless possibly the Pandanaceæ.

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EXPLANATION OF PLATE XLVI.

All figures except 1 and 4 were studied with Leitz lenses and drawn with a Zeiss camera. All figures slightly reduced.

Figs. 4, 5, 7, 15 and 23 refer to *Sparganium Greeni* Morong, the others to *S. simplex* Huds.

Fig. 1. Two female flowers of *S. simplex* enlarged about eight times; the one at the right with the perianth removed.

Fig. 2. A single scale of the perianth more enlarged.

Fig. 3. Longitudinal section of the ovary showing the single ovule; ***ma***, embryo-sac. Oc. 1, obj. 3.

Fig. 4. Pistil of *S. Greenii;* × about 8.

Fig. 5. Section of the ovary of *S. Greenii*. Oc. 1, obj. 3.

Fig. 6. Sections of ripe pollen-spores of *S. simplex*, showing the large vegetative, and smaller generative, nucleus; ***pr***, prothallial cell. Oc. 1, im. $\frac{1}{18}$.

Fig. 7. Sections of younger pollen-spores of *S. Greenii;* the nucleus is still undivided, and no prothallial cell is visible. The clear space on the surface probably marks the place of exit of the pollen-tube.

Fig. 8. Upper part of the embryo-sac of *S. simplex* just after the entrance of the pollen-tube; *o*, the egg-cell; *sy*, one of the synergidæ; ***pt***, pollen-tube. Oc. 1, im. $\frac{1}{18}$.

Fig. 9. Another section of the same embryo-sac; the small dark body within the synergid is probably one of the generative nuclei from the pollen-tube.

Fig. 10. The antipodal end of the same embryo-sac, showing the single large endosperm-nucleus and two of the antipodal cells.

Fig. 11. The egg-apparatus and endosperm-nucleus from a mature embryo-sac. Oc. 1, im. $\frac{1}{18}$.

Fig. 12. (*a*) Two antipodal cells from a mature embryo-sac; (*b*) outline showing the position of the three small antipodals. Oc. 1, im. $\frac{1}{18}$.

Fig. 13. Section of the egg-apparatus showing the entrance of the pollen-tube, ***pt***. A small body (the generative nucleus ?) is visible within the egg; both synergidæ are still intact. Oc. 1, im. $\frac{1}{18}$.

Fig. 14. Another section of the same; the pollen-tube has apparently discharged a small granular mass into the embryo-sac.

Fig. 15. Section of the nucellus and mature embryo-sac of *S. Greenii*. Oc. 1, obj. 7. A large cell (an extra antipodal ?), lies above the three antipodal cells.

Fig. 16. The antipodal region of fig. 16 more highly magnified.

Figs. 17 and 18. Two sections of the egg-apparatus of *S. Greenii*. Oc. 1, im. $\frac{1}{18}$.

Fig. 19. Embryo-sac of *S. Greenii*, showing egg, *o*, and two antipodals, ***ant***. Oc. 1, obj. 7.

Fig. 20. Unusually large sac of the same species; the section shows the two synergidæ and the still separate polar nuclei. Oc. 1, obj. 7.

Fig. 21. Two of the antipodal cells from the same sac more highly magnified.

Fig. 22. Section of egg-apparatus of *S. Greenii*. Oc. 1, im. $\frac{1}{18}$.

Fig. 23. Endosperm-nucleus from a similar sac.

EXPLANATION OF PLATE XLVII.

Figs. 33–36 refer to *S. Greenii*, the others to *S. simplex*.

Fig. 24. Apex of fertilized embryo-sac with one-celled embryo. Oc. 1, im. $\frac{1}{18}$.

Fig. 25. An embryo of the same age, but with a broader base of attachment. One synergid could be still made out.

Fig. 26. A recently fertilized embryo-sac; one of the enlarged antipodals, *ant.*, is shown. The endosperm-nucleus has divided once. Oc. 1, obj. 7.

Fig. 27. The antipodal region of the same more highly magnified; the three enlarged antipodal cells lie in the same plane; one of the two endosperm-nuclei is shown.

Fig. 28. Enlarged antipodal cells from an older sac; each of the cells shown has two nuclei; the whole number of nuclei was eight or nine. Oc. 1, im. $\frac{1}{18}$.

Fig. 29. Two sections of the antipodal group from a still older sac; some of the nuclei are dividing; twelve antipodal nuclei could be distinguished. Oc. 1, im. $\frac{1}{18}$.

Fig. 30. Nearly median section of the antipodal group from a much older sac. Oc. 1, obj. 7. Divisions have formed between all the nuclei; numerous free endosperm-nuclei, *en.*, are present.

Fig. 31. Part of the lining layer of protoplasm with a single endosperm-nucleus. Oc. 1, im. $\frac{1}{18}$.

Fig. 32. Surface view of a portion of the nucleated protoplasmic layer lining the wall of the embryo-sac.

Fig. 33. Antipodal cells from the unfertilized sac of *S. Greenii*. Oc. 1, im. $\frac{1}{18}$.

Fig. 34. Antipodal group shortly after fertilization; the upper cell has enlarged and divided; the two lower ones show indications of disintegration.

Fig. 35. Antipodal group of *S. Greenti* in which all the cells appear active.

Fig. 36. A somewhat older group of the same species; growth is mainly confined to the upper cell.

Fig. 37. Upper end of embryo-sac of *S. simplex* showing the young embryo surrounded by the endosperm-cells; the central nuclei, *en*, are still free. Oc. 1, obj. 7.

Fig. 38. The embryo from fig. 37 more enlarged.

Fig. 39. Median section of a similar embryo. Oc. 1, im. $\frac{1}{18}$; *xx*, the basal wall.

Fig. 40. Series of three cross-sections of an embryo of about the same age; *a*, the lowest segment.

Fig. 41. Two sections of an older embryo, cut in the plane of the cotyledon. Oc. 1, obj. 7.

Figs. 42, 43. Longitudinal sections cut at right angles to the plane of the cotyledon; the basal wall is decidedly oblique. Oc. 1, obj. 7.

Fig. 44. Three cross-sections of an embryo of about the same age as 42; the lowest segment is divided into four cells. Oc. 1, obj. 7.

Fig. 45. Upper part of embryo-sac showing the embryo surrounded by the densely granular endosperm-cells; the granular cell-contents of the embryo are not shown. Oc. 1, obj. 7.

Fig. 46. The same embryo shown in fig. 45, showing the differentiation of the primary tissues, the plerome ends at the basal wall, *xx*.

Fig. 47. A transverse section of an embryo of about the same age. Oc. 1, obj. 7.

Fig. 48. Section in the plane of the cotyledon of a similar embryo, with very regular arrangement of the tissues. Oc. 1, obj. 7.

Fig. 49. Median section of an older embryo, showing the stem-groove, *st*. Oc. 1, obj. 7.

Fig. 50. Embryo of about the same age, cut in the plane of the cotyledon.

Fig. 51. Median section of the base of the same embryo, more highly magnified; *pl.*, the plerome.

EXPLANATION OF PLATE XLVIII.

All figures except 69, refer to *S. simplex*.

Fig. 52. Two sections of a nearly mature embryo. Oc. 1, obj. 3.

Fig. 53. Root-end of a somewhat younger embryo. The position of the original transverse, or basal wall (*x*) is still evident, l^2, the second leaf; *st.* the stem-apex. Oc. 1, obj. 7.

Fig. 54. Three cross-sections of a mature embryo. Oc. 3, obj. 3.

Fig. 55. Sections of the young seed before the endosperm has filled the embryo-sac; *e*, embryo; in^1, in^2, integuments.

Fig. 56. Section through the layer of developing endosperm lining the embryo-sac; many of the nuclei are dividing. Oc. 1, obj. 7.

Fig. 57. Larger endosperm-nuclei from the base of the sac at the time the walls are first beginning to form; some of the nuclei have more than one nucleolus; the fine fibres connecting them are plainly visible. Oc. 1, im. $\frac{1}{18}$.

Fig. 58. Transverse section of recently formed endosperm-cells showing the nucleolus fragmenting. Oc. 1, im. $\frac{1}{18}$.

Fig. 59. Upper part of the young seed showing the enlargement of the micropylar portion of the integuments. Oc. 3, obj. 3.

Fig. 60. Young sclerenchyma-cells from the pericarp. Oc. 1, obj. 7.

Fig. 61. Fully developed sclerenchyma-cell showing the deeply pitted walls. Oc. 1, obj. 7.

Fig. 62. Surface view of the pits more highly magnified.

Fig. 63. Endosperm-cells from nearly ripe seed, showing large crystalloids. Oc. 1, obj. 7.

Fig. 64. Separate crystalloids more highly magnified.

Fig. 65. Abnormal embryo-sac of *S. simplex;* the sac divided longtudinally with the endosperm-nucleus on one side. Three antipodals could be distinguished. Oc. 1, obj. 7.

Fig. 66. Micropylar end of the same sac.

Fig. 67. One of the antipodal cells of the same.

Fig. 68. Abnomal embryo-sac (perhaps unfertilized?); there has been little increase in size of the sac, but numerous endosperm-nuclei are present, and the antipodals have enlarged and divided. Oc. 1, obj. 7.

Fig. 69. Two sections of an abnormal embryo-sac of *S. Greenii;* three antipodals could be seen, and the polar-nuclei (*p.n.*), in close contact, were separated from the body of the sac. The upper part was also shut off by a membrane, and no definite egg-apparatus could be distinguished. Oc. 1, im. $\frac{1}{18}$.

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XXII

The Development and Phylogeny of Placenticeras

BY

JAMES PERRIN SMITH
Stanford University, California

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1900

PREFATORY NOTE.

This memoir is the twenty-second of a series designed to illustrate investigations and explorations connected with the Hopkins Seaside Laboratory, an adjunct of the biological laboratories of the Leland Stanford Junior University. These investigations have been carried on by means of the assistance given by Timothy Hopkins, Esq., of Menlo Park, California. This memoir appears in the publications of the California Academy of Sciences, the present edition being a reprint.

OLIVER P. JENKINS,
CHARLES H. GILBERT,
Directors Hopkins Laboratory.

Date of publication, Aug. 15, 1900.

THE DEVELOPMENT AND PHYLOGENY OF PLACENTICERAS.

BY JAMES PERRIN SMITH.

Stanford University, California.

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August 4, 1900.

INTRODUCTION.

THE interest of the paleontologist in embryology, and in ontogeny in general, lies wholly in the desire to know the origin and relationships of biologic groups. A scientific interpretation of ontogenic data in terms of phylogeny depends on the extent of preservation of the ancestral record in individual development. The broad statement has often been made that each animal gives in its own development an epitome of the history of its race. Because of the law of heredity, this statement would be true, and the record would be complete, if nothing had interfered with the normal course of things. But, in reality, so many secondary elements are introduced in development, that authorities are very much divided as to the value of ontogenic stages as records of race history.[1]

There can be no doubt that students of postembryonic stages have been inclined to claim too much for the law of tachygenesis, while, on the other hand, students of embryology have been inclined to discredit it almost entirely, and to lay little stress on ontogenic stages as a recapitulation of phylogeny. The reason for this disagreement is not far to seek; it lies in the field and in the methods of research of the two groups of morphologists.

Types of Development.—Leaving out of consideration the *Protozoa*, which come into being with the essential characteristics of the adults, there are, in the *Metazoa*, two types of development: (1) the *fœtal type*, in which development takes place in the egg, or in the body of the parent, and the young animal comes into the world in form closely resembling the adult; (2) the *larval type*, in which the young animal comes out at an earlier stage of development, and reaches maturity only after considerable metamorphosis.

Secondary elements will be introduced in either type of development, and those variations that are favorable to the preservation of the species are likely to be perpetuated by heredity. Now in the fœtal type the most favorable variation consists in abbreviation, thus simplifying the development. Any characters that are useful in a free state, but not in a fœtal state, are liable to be lost. Thus in the fœtal type the tendency is towards loss of the record through omission of stages or obscuring them, for many organs that would be highly developed in mature forms, or in free larvæ, will be either suppressed or undifferentiated.

---

[1] In the preparation of this Introduction the writer has drawn largely on Balfour's "Treatise on Comparative Embryology," and on Lang's "Comparative Anatomy."

The vertebrates, most of the higher crustaceans, most land and fresh-water molluscs[1] have the fœtal type of development; and these embrace by far the larger part of animals whose ontogeny has been studied. It is not to be wondered at, then, that morphologists who deal exclusively with embryonic stages of these groups should be sceptical about the repetition of family history in individual development. Here many stages are omitted, and the rest so obscured and undifferentiated as to be unintelligible; and secondary characters, due to life in the egg or in the parent, are introduced, effacing what little meaning was left. Then, too, embryologists are often content to trace the animal but a little way toward perfection of development; they study the embryo until the cells begin to divide into groups indicating a beginning of organs, and call this studying ontogeny, when they have stopped before it could be told whether the animal was going to develop into fish, flesh, or fowl. To this sort of study is due the idea of "falsification of the record," a crime of which nature has not yet been guilty, although she at times may not, perhaps, have told the whole truth.

Primary and Secondary Larvæ.—If the way of the embryologist lies in stony places, that of the student of post-embryonic stages is not much smoother; formidable obstacles meet him on every side, reducing his small stock of faith. At the very outset he is confronted by the difficulty that there are two distinct types of larvæ: *(a) primary*

---

[1] *Dreissensia*, a fresh-water pelecypod, which in very recent geologic time has immigrated from salt-water, still goes through its larval development, like its marine relatives.

larvæ, such as are more or less modified from ancestral forms, and have continued to develop as free larvæ since the time when they constituted the adult forms; *(b) secondary larvæ*, such as have been introduced by kenogenesis into the ontogeny of species that formerly developed by the fœtal process. If ancestral characters have been retained in the egg, then these secondary larvæ may bear some palingenetic characters, and thus be hard to distinguish from primary larvæ; otherwise they will be entirely adaptive, or kenogenetic. A case in point is the development of most insects, whose larval stages are supposed to be entirely secondary. Study of individual development in a group of this sort can throw no light on phylogeny.

The student of larval stages must confine himself to the primary sort, if he would correlate them with ancestral genera. The development of the cœlenterates, echinoderms, brachiopods, most molluscs, and the lower crustaceans is direct; thus larval stages of these groups may be bearers, to a greater or less degree, of ancestral characters. But since the free larvæ of even these groups are exposed to natural selection, secondary or kenogenetic characters will be introduced, obscuring the resemblance to ancestral forms; also characters that in the adult ancestral form were functional and fully developed may in the representative larval stage of the descendant be so little differentiated as to be unrecognizable.

But how can the morphologist who deals entirely with living species know whether a character is primary, and repeated by palingenesis in the larval history of the descendant, or whether it is secondary, and introduced by kenogenesis into that history? The answer to this lies wholly within the domain of paleontology, for only by finding a stage of growth represented by an ancestral form can the morphologist know that the characters of that stage are ancestral, and not secondary. Larval stages which may be the bearers of ancestral characters must then be compared with the adults of their predecessors, and the paleontologic record must be invoked as a final resort—the court from which there is no appeal.

And this was exactly the method used by Louis Agassiz, who first applied the law of acceleration of development to the study of systematic zoology, although it never had much influence on biologic investigation until the paleontologic studies of Hyatt (1872) in the invertebrates, and Cope in the vertebrates placed the law on a sound basis. It was reserved for Alpheus Hyatt (1866) to formulate the law, and to strengthen theory with practical examples based on study of Cephalopoda. In his later papers Professor Hyatt (1889, preface, p. ix) has given a more exact and comprehensive definition of the law of acceleration or *tachygenesis:* "All modifications and variations in progressive series tend to appear first in the adolescent or adult stages of growth, and then to be inherited in successive descendants at earlier and earlier stages according to the law of acceleration, until they either become embryonic, or are crowded out of the organization, and replaced in the development by characteristics of later origin." A still more definite statement by the same author (Hyatt, 1894) is the following: "The substages of development in ontogeny are the bearers of distal ancestral characters in inverse proportion and of proximal ancestral characters in direct proportion to their removal in time and position from the protoconch or last embryonic stage."

To insure trustworthy results in verifying this law, the investigator must have groups in which the larvæ are primary and reproduce ancestral characters; in which the living and the fossil are classified on the same basis; of which we have preserved a nearly complete geologic record; and of which material is available for the study of fossil ontogeny as a check on the living. Such groups are especially represented among the *Cœlenterata*, the *Echinodermata*, the *Brachiopoda*, and the *Pelecypoda* and *Cephalopoda* among the molluscs.

Unequal Acceleration.—Now, when the morphologist has settled the fact that primary larval stages do actually reproduce, more or less vaguely, characters that existed in the adult forefathers of the generation he is at work on, his troubles are even then not yet ended; for the characters do not necessarily appear in the ontogeny of the descendant in the same association in which they occurred in the ancestor. A character useful to the immature form will have a tendency to be inherited at an earlier age than those useful only to the adult, and so by unequal acceleration of development the parallel between ontogeny and phylogeny is broken. It was once thought that the *Nauplius* larva of the crustaceans was a mature genus, then it was thought to be a larval representative of the extinct radicle of the Crustacea; later still, many morphologists have concluded that the *Nauplius*, while it bears many crustacean characters, still retains too many annelid characters to represent the radicle of the group; it is a typical crustacean larva, but not a representative of the primitive crustacean, and the two sets of characters are thrown together by unequal acceleration. Beecher (1895, p. 173, Pl. IX, figs. 1, 2, 4) has shown the same thing in the spiny larvæ of *Acidaspis* and *Arges*, where in the protaspis of these genera the spines characteristic of the adults appear, contrary to usage among the trilobites, in which larval stages are usually smooth. Thus before these animals have assumed characters that would identify them undoubtedly with trilobites they have assumed those most characteristic of their own genera. Jackson (1890, p. 381) has shown that in the larvæ of the *Pectinidæ* unequal acceleration may associate characters that were not synchronous in race history. F. Bernard (1896–97) has recently shown that the prodissoconch of pelecypods is sometimes striated and ribbed, characters that could not have belonged to the primitive pelecypod.

If unequal acceleration causes confusion in the phylembryonic stages, the difficulty is much greater in the larval and adolescent periods, where the shortness of the time of development causes throwing together of characters that were not contemporaneous in the ancestors, and where the small size and general habits prevent differentiation of organs that in the correlative adult forms were highly developed, thus obscuring and even destroying the exactness of the parallelism.

The two species of *Placenticeras*, of which the ontogeny is described in this paper, must have descended not only from the same perisphinctoid family, but also from the same species of *Hoplites;* and thus if the parallel were at all exact, they should be alike in the late adolescent stages, when they begin to show their generic characters. This, however, is not the case, for they are quite different throughout the cosmoceran stage, and back almost to the end of the larval period, where the transition from goniatite to ammonite took place. If this were interpreted without taking account of unequal acceleration, it would seem that the differentiation of the two species took place back in the Trias, and that different ægoceran forms were the remote ancestors of the two species, which we know could not have been the case.

The writer (1899) has recently worked out the ontogeny of two very nearly related species of *Schlœnbachia*, one of which, in its larval period, reproduces very exactly a *Paralegoceras* stage, while the other does not; the latter species has, however, all the paralegoceran characters, but associated with others that this genus never had, but which belonged to later descendants of this genus. There can be here no question of the veracity of nature in keeping the record, the difficulty lies in deciphering it. So it is not to be expected that any one species would give in plain terms the complete phylogeny of a genus, for stages that are plainly differentiated in one will be obscured in another, and only by studying the ontogeny of a number of species of one genus can the morphologist hope to get a complete history.

Retardation.—Another factor that makes it difficult to correlate ontogeny and phylogeny is *retardation* of development. Cope first recognized the principle, but in his writings confused it with unequal acceleration, and since his reasoning was purely theoretical the idea has never gained much foothold in biologic philosophy. Cope's statement (1887, p. 142) of the theory is as follows: "The acceleration in the assumption of a character, progressing more rapidly than the same in another character, must soon produce, in a type whose stages were once the exact parallel of a permanent lower form, the condition of inexact parallelism. As all the more comprehensive groups present this relation to each other, we are compelled to believe that *acceleration* has been the principle of their successive evolution during the long ages of geologic time. Each type has, however, its day of supremacy and perfection of organism, and a retrogression in these respects has succeeded. This has, no doubt, followed a law the reverse of acceleration, which has been called *retardation*. By the increasing slowness of the growth of the individuals of a genus, and later and later assumption of the characters of the latter, they would be successively lost.'' This statement of Cope might apply equally well to unequal acceleration of characters, but in another part of this same work he gives a clearer statement: '' Where characters which appear latest in embryonic history are lost, we have simple retardation, that is, the animal in successive generations fails to grow up to the highest point of completion, falling further and further back, thus presenting an increasingly slower growth in the special direction in question.'' (Cope, 1887, p. 13.)

These remarks of Cope were based on abstract reasoning, but it is possible to bring up some striking cases in support of the theory, notably among the brachiopods. Fischer and Oehlert (1892) have shown that while brachiopods go through many metamorphoses in individual evolution, and while each species is usually constant in the stages it goes through, it often happens that the individual is arrested in development, never reaching the full generic development of the mature stage. The individual then begins to reproduce its kind before maturity is reached, and tends to give rise to a stock that never reaches the full generic evolution of its ancestors. Dr. C. E. Beecher (1893*b*) has well described this: ''In each line of progression in the Terebratellidæ the acceleration of the period of reproduction, by influence of environment, threw off genera which did not go through the complete series of metamorphoses, but are otherwise fully adult, and even may show reversional tendencies due to old age; so that nearly every stage passed through by the higher genera has a fixed representative in a lower genus. Moreover, the lower genera are not merely equivalent to, or in exact parallelism with, the early stages of the higher, but they express a permanent type of structure, so far as these genera are concerned, and after reaching maturity do not show a tendency to attain higher phases of development, but thicken the shell and cardinal process, absorb the deltidial plates, and exhibit all the evidences of senility."

If, then, the morphologist tries to study the race history in one of these species thus arrested in development, he can not read the whole story, for the individual ontogeny will not recapitulate the higher stages lost by retardation.

Another remarkable case is that of the so-called "ceratites" of the Cretaceous. While there have been no goniatites since the Paleozoic, and no ceratites since the Trias, there are found among the ammonites of the Cretaceous some with septa of simple goniatitic character, and others with septa like those of the genuine ceratites. Now since the line of descent is broken and there is no possibility for a continuous line of these ancient primitive forms to have bridged over the great gap from the Trias to the Upper Cretaceous, we must explain this either by reversion, or in some other way. But it is not a simple case of reversion, for, as has been pointed out by several writers (Douvillé, 1890, pp. 275–292; Nicklès, 1890), the septum of adolescent ammonites of this group is not more complex, but really less so, than that of adults, although they are derived from Jurassic genera with complex septa. Thus Douvillé, in the paper cited above, derives the group *Placenticeras-Sphenodiscus* from *Hoplites;* the Pulchellidæ, composed of *Pulchellia*, *Neolobites*, and *Tissotia*, he derives from *Oppelia* of the Jura. Since in each case the ancestral forms are more complex than the descendants, the reduction in complexity of generic evolution can be explained only by retardation, or arrested development. F. Bernard (1895, p. 668) has, in addition, pointed out the fact that the adult of *Pulchellia* is like the adolescent stage of the ancestral *Oppelia*. Now, if we define the law of acceleration of development to mean that in a progressive series the young of the descendants correspond to the adults of their more remote ancestors, we find that this does not apply to a retrogressive (retarded) series. In this latter case we must restate the law as follows: The adults of descendants correspond to the young of their more remote ancestors, the higher generic stages to which these ancestors attained having been dropped away by successive retardation, or arrested development. The retarded series themselves may become the radicles of new stocks, and so we may have cases where the ontogeny of any one species or genus can never give the full history of the race.

Groups Available for Correlation.—We see, then, that the student of morphogeny of animals has to be on his guard, first against the loss of generic stages during the period while the animal is in the egg; then against the introduction of secondary larval stages when the ancestors lacked them; then against the introduction of secondary characters due to adaptation; then against unequal acceleration, bringing together, in the ontogeny of the descendant, characters that occurred in separate generations of ancestors; and lastly, against retardation, by which the form never reaches the full generic evolution of its ancestors, and where, if a new series starts out from the retarded form, the complete family history is not recorded in ontogeny.

Is it to be wondered at, then, that the student of morphology becomes a sceptic, or even a rank unbeliever with regard to the value of ontogenic stages as records of history? It is only to be expected that the biologist, especially one that deals almost exclusively with living species, should be inclined to discredit the law of tachygenesis, and to believe that there is such an inextricable muddle of omissions, secondarily introduced characters, and unequal acceleration of those actually repeated, that the record is wholly untrustworthy, or at least illegible. And yet there are so many species and genera in the various groups of invertebrates whose ontogeny is simple, progressive and fairly complete, and whose stages of growth are almost exact repetitions of successive antecedent genera, that it would be impossible to find a student of the morphogeny of the brachiopods, the marine molluscs, or the lower crustaceans, that does not believe implicitly in the value of larval stages of these groups as records of their family history. And this is especially true of the paleobiologists, who regard it of little importance whether the animal under investigation died yesterday, during the Flood, or during the Paleozoic era, whether it is preserved in alcohol or in a more permanent museum in the bosom of Mother Earth; they recognize the fact that the laws that govern the rise and decline of organisms were just as true then as now, and that the life-history of a Cambrian trilobite has as much bearing on modern biology as does the history of the living cray-fish.

Not all groups are equally useful to the student of morphogeny, but in each of the lower subkingdoms there are genera of which the ontogeny has been worked out and correlated in no uncertain terms with the history of the race. The testimony of these various groups is so uniform, notwithstanding the fact of its having been gathered by men of different beliefs, that its value can not be doubted. It is also noteworthy that in the higher groups, such as cephalopods and crustaceans, the evidence and the correlations are much more decided.

Cœlenterata.—It has been shown by Dr. C. E. Beecher (1891) that the young stages of the Favositidæ correspond to *Aulopora*, or to some other similar unspecialized genus. This same conclusion has been reached by Dr. G. H. Girty (1895) based on a study of the ontogeny of *Favosites*, *Syringopora*, and other tabulate corals, all of which are shown to go through an *Aulopora* stage of growth.

Echinodermata.—The only crinoid of which the ontogeny is known is *Antedon*, which has been shown by Sir Wyville Thomson (1865) to go through successively stages corresponding to the *Ichthyocrinoidea* of the Paleozoic, and *Pentacrinus* of the Mesozoic, before it becomes free swimming and takes on the characters of *Antedon*.

Dr. R. T. Jackson (1895) has been able to prove even in the Paleozoic sea-urchins the possibility of correlating growth stages with phylogeny, in spite of the great difficulties due to resorption of plates, and change of form.

Brachiopoda.—According to Beecher (1891, 1892) all brachiopods go through a primitive protegulum stage, correlative with the supposed ancestor of the class, although *Paterina*, which was formerly supposed to be this radicle, has been shown to be much more highly specialized than the protegulum stage. The later stages of growth of this class are capable of even more remarkable correlation, as has been shown by Beecher (1893*a*) in a number of papers, where every stage of growth is distinctly homologous with well known pre-existing genera; and these same successive genera show a gradual transition in the adults.

Even among the Paleozoic spire-bearers *(Helicopegmata)*, this holds good, for Beecher and Schuchert (1893) have demonstrated that the early stages of this group are homologous with the terebratuloids *(Ancylobrachia)*, and more especially with the Paleozoic genus *Centronella*, the most primitive of the loop-bearing brachiopods.

Mollusca.—Jackson's correlations of the stages of growth of pelecypods (1890) with their race history have already become classic; according to these, every pelecypod begins its bivalve state with a nuculoid stage, homologous with the primitive radicle of the group. Every *Pecten* goes through stages successively correlative with a nuculoid, *Rhombopteria*, *Pterinopecten* and *Aviculopecten*, before it reaches maturity, each stage appearing in the order of the ancestral genus. Even the greatly modified oyster shows its kinship with this group by its nuculoid and *Rhombopteria* stages.

The researches of Branco have made it clear that each group of cephalopods has its typical phylembryo, in a general way correlative with the radicle of the group, and that the later stages may be compared very accurately with ancestral families and genera. The way for this was opened by Hyatt's memoirs on the ontogeny of the ammonites, in which it was shown that in each perfect adult ammonite shell the complete individual ontogeny is recorded. By using this same method Karpinsky (1889) has been able to correlate the ontogeny of *Medlicottia* and *Pronorites* with successive ancestral forms, from *Anarcestes*, *Ibergiceras*, *Paraprolecanites*, up to the adult stage.

By the ontogenic method Buckman has been able to get at a sound basis of classification of the Jurassic ammonites, and to correlate the growth stages of many of these with their race history. Although his conclusions as to the systematic position of many of these genera do not agree with the ideas commonly accepted concerning them, it must not be forgotten that these conclusions are based, not merely on ontogenic study alone, but also on the gradual transitions of a series of adults. This is the strongest confirmation that any phylogenic research could ever have.

Crustacea.—Among the most convincing morphogenic researches are Beecher's studies (1895) in the ontogeny of the trilobites, all of which are shown to go through a phylembryonic *protaspis* stage, correlative with the primitive crustacean, and similar to the protonauplius of the less specialized living crustaceans. Here, too, it was demonstrated that the larval and adolescent stages of Devonian, Silurian, and even Cambrian trilobites may be correlated with the adults of pre-existing genera, giving the basis of a natural, or biogenetic, classification of this extinct group.

Many more cases might be added to those cited here, but surely no additional evidence is needed, for all this points in the same direction, whether gathered by believers in or by opponents of the theory of evolution. To this latter class belongs the evidence brought forward by Barrande (1852) in the ontogeny of trilobites, and by Agassiz in the law of recapitulation or acceleration of development. Each of these naturalists used unhesitatingly the method that in the hands of Hyatt and his followers has been so fruitful of results.

AFFINITIES OF PLACENTICERAS AND HOPLITES.

The genus *Placenticeras* was established by F. B. Meek (1876) to include large, discoidal, compressed shells, with narrow umbilicus, narrow, flattened abdomen, and rows of knots forming a pair of marginal keels on the abdomen; shell with obscure knots or ribs, but with fine sigmoid lines of growth; septa divided into a large number of lateral lobes and saddles, increasing in size up to the third, and decreasing from that toward the umbilicus. The type of the genus was *Placenticeras placenta* Dekay, of the Fort Pierre group, Upper Cretaceous. Along with the type species Meek included in this group also *P. andoorense* Stoliczka, *P. guadaloupæ* Roemer, and *P. orbignyanum* Geinitz, all from the Cretaceous. Meek did not attempt to place *Placenticeras* in any of the so-called families of ammonites, but by almost universal consent paleontologists have grouped it with the Amaltheidæ (Zittel, 1885, p. 452; 1895, p. 407; Steinmann, 1890, p. 416), along with the so-called "Ceratites" of the Cretaceous, on account of a certain resemblance to the Jurassic forms with beaded abdominal keels. This, however, was before the days when paleontologists looked upon the development of ammonites as the key to their systematic position, and taxonomy made little pretense of being biogenetic.

The first dissenting voice was raised by H. Douvillé, in a paper "Classification des Cératites de la Craie" (1890), where the opinion was expressed that *Placenticeras* and *Sphenodiscus* both developed out of the group of *Hoplites-Sonneratia*. F. Bernard (1895, p. 676) has accepted this view, placing the genus under the Stephanoceratidæ. Unpublished researches of the writer show, however, that *Sonneratia* and *Desmoceras* are much more closely allied to *Stephanoceras* than is *Hoplites*, from which group *Placenticeras* originated. *Hoplites* is considered by the writer, not as originating from the Stephanoceratidæ, but as having a common origin with that family in the Ægoceratidæ.

The species from the Lower Cretaceous commonly assigned to *Placenticeras* mostly belong to *Oppelia*, to *Sphenodiscus*, and to other genera. Not every keeled, discoidal ammonite can be placed here, for it is well known that among the ammonites mere resemblance is not proof of near kinship. Sarasin (1893) has shown that *Ammonites* *nisus* d'Orb. belongs to *Oppelia*, and that there are several series of these plate-shaped ammonites, commonly ascribed to the Amaltheidæ, but in reality derived from wholly different groups.

The true species of *Placenticeras*, that is of the type of *P. placenta*, are descendants of *Hoplites*, and thus have no kinship with the Amaltheidæ; this is the opinion of H. Douvillé, and it has been fully confirmed by an ontogenic study of two species. These species had been under investigation by the writer for a long time before their real affinities were found out; the largest specimens obtained were between 20 and 30 millimetres in diameter, and were naturally supposed to be adults, for on the last coil there was no further progressive development. One species was remarkably like *Hoplites dufrenoyi*, and the other like *H. splendens*, both of the Gault; thus they were assigned to *Hoplites*, although the premonition of *Placenticeras* was shown in the provisional name, "*H. placenticeratoides*," given by the writer, and in the unpublished description, in which it was said that this species was tending decidedly toward becoming a *Placenticeras*, although it had not yet quite developed beyond the limits of *Hoplites*. After this was written, although luckily not published, the writer obtained a number of larger specimens of both species, up to 170 millimetres in diameter, showing a perfect and gradual transition between the two genera.

The earliest known species of *Placenticeras* occur along with *Sphenodiscus* in the zone of *Mortoniceras rostratum (=Schloenbachia inflata)*, in the Albian stage, upper Gault, top of the Lower Cretaceous. Thus the genus must have developed out of *Hoplites* in the upper part of the Lower Cretaceous. Now since the origin and affinities of *Hoplites* are pretty well known, a discussion of this genus becomes of prime importance in an investigation of the derivation and systematic position of *Placenticeras*.

The genus *Hoplites* was established by Neumayr (1875) to include forms with rather compressed flattened sides, high whorls, moderately narrow umbilici, sinuous lateral ribs with umbilical and marginal knots or spines, and usually with a furrow interrupting these ribs on the abdomen, often forming a pair of shoulder keels. The septum is finely and deeply divided; in addition to the first and second lateral lobes there are one or more auxiliary lobes, and the two lateral saddles are deeply divided by secondary lobes.

This genus, which Neumayr supposed to have originated from *Perisphinctes*, included many species that have since been placed in other genera, in some cases even in other families, but after the segregation from it of *Sonneratia* Bayle, *Stoliczkaia* Neumayr, *Pulchellia* Uhlig, there is still left a large number of species, showing great variation in form and other characters, which may, after all, not belong to a monophyletic genus. Zittel (1885, p. 475; 1895, p. 428) first classed *Hoplites* with the Stephanoceratidæ; then in a later work, with the Cosmoceratidæ, along with *Cosmoceras* Waagen, *Parkinsonia* Bayle, *Sonneratia* Bayle, and *Acanthoceras* Neumayr, as a side branch from the Stephanoceratidæ. Zittel is inclined to the belief that *Cosmoceras* is the direct ancestor of *Hoplites*, an opinion which seems to be the more correct, for the two species of *Placenticeras*, of which the ontogeny is described in this paper, show a decided *Cosmoceras* stage in the adolescent period just before the *Hoplites* stage, and one of them retains some of these characters until maturity. In each case this stage begins by a sudden stopping of the perisphinctoid ribs on the abdomen, the formation of strong knots on the angular abdominal shoulders, and a sharper forward bending of the lateral ribs, which fork near the shoulders, forming the beginning of a second row of knots. At this stage one can see a resemblance, not to the exaggerated species of *Cosmoceras*, such as *C. ornatum*, *C. jason*, or *C. elizabethæ*, but rather to some simpler form; it is not possible to refer to any particular species as the ancestral form, nor is it likely that any one species was the only one that developed the style of rough ornamentation that is called *Hoplites*.

F. Bernard (1895, p. 673) agrees substantially with Zittel as to the systematic position of the genus, as do also most other writers on the subject; Steinmann (1890, p. 445) groups it in the Ægoceratidæ, subfamily Perisphinctinæ, division *(b)* Tuberculati, along with *Acanthoceras* and *Holcodiscus*. All these writers connect the genus with *Psiloceras* as the radicle from which the entire perisphinctoid stock sprang, although the opinion is based, not on ontogenic study, but purely on the geologic succession of types, a satisfactory method only where the paleontologic record is very complete.

In a later paper Sarasin (1897) concludes, as a result of ontogenic study, that *Hoplites* is not a member of the highly specialized Stephanoceratidæ, but comes from the more primitive perisphinctoids along with *Desmoceras*. Most writers agree that the perisphinctoids come from the Ægoceratidæ, that they, in turn, are derived from *Psiloceras*, and that this genus branched off from the Phylloceratidæ. E. Haug (1894) expresses the opinion that not only the Ægoceratidæ, but also the Amaltheidæ, the Arietidæ, and most of the other Jurassic stocks were derived from the Phylloceratidæ, because their septa are triænidian in early youth, and megaphyllian in the development of the principle saddles. This seems to be nearer the mark, although the descent must be from some of the earlier unspecialized forms of the Phylloceratidæ, such as possibly *Monophyllites*, although certainly not from any known species of that genus; at any rate, none of these genera show a *Psiloceras* stage in their ontogeny. S. S. Buckman (1898, p. 445), contrary to the general opinion, says that *Psiloceras* is not the ancestor of the Arietidæ nor the Ægoceratidæ, but is, itself, a degenerate form.

The immediate ancestors of the Ægoceratidæ may be sought among the Polymorphidæ, a group established by E. Haug (1887) to include a number of the more primitive ammonites of the Lias. *Agassizceras*, the principal genus of the group, is considered by Hyatt (1889) to be the immediate ancestor of the agassizceran branch of the Arietidæ, and the direct descendant of *Psiloceras*. Neumayr (1878) segregated a number of the simpler species of this group under the name of *Cymbites*, characterized by rather globose form, very slightly ammonitic septa, and absence of ventral keel. Hyatt (1889) says *Cymbites* is probably only the young of *Agassizceras*, while Haug considers the characters upon which Neumayr based the genus not to be sufficiently constant to warrant the separation, although he regards the problematic species as adult forms. However this may be, we know that the young of the more specialized Polymorphidæ are like *Cymbites*, and whether the forms described by Neumayr were adults or not, there must have been such a genus as ancestor of the group, and not only of this small section, but also of the Ægoceratidæ as well; so it will be well to retain *Cymbites*, although Buckman leaves this genus out of the Polymorphidæ, which he does not consider the primitive family.

Another form that may possibly be in the genetic series of the Ægoceratidæ, and thus of *Placenticeras*, is the genus *Diaphorites* Fucini (1896, *a* and *b*, p. 232, Pl. XXV, figs. 1–15), which, although small, is surely made up of adult forms. This genus greatly resembles *Cymbites*, and is thought by Fucini to be genetically connected with the Phylloceratidæ; the youthful stages of *Diaphorites vetulonius* Fucini, as described and figured by that author, are remarkably like the young of *Placenticeras pacificum*, sp. nov., figs. 13 and 14 of Fucini's paper, reproducing exactly the glyphioceran stage, and fig. 12 is like the *Nannites* stage of *Placenticeras*. The early adult septa of *Diaphorites*, copied on plate XXVIII, fig. 7, after Fucini, are almost exactly like the early adolescent septa of *Placenticeras*, and the parallel is also quite exact as to form and sculpture. As only one species of the genus is known as yet, and that only in Italy, it would be premature to single this out as the connecting link between the perisphinctoid group, and the phylloceran stock; the most we can say is that this connecting link must have been some such genus.

Fucini (1896, *a* p. 124, and *b* p. 236, Pl. XXV, figs. 16–21) has described another genus, *Pimelites*, that might possibly be the radicle of the ægoceran stock; it is very like *Diaphorites*, differing only in some unimportant characters, and being, in Fucini's opinion, intimately related to the

Phylloceratidæ, and regarded as a possible ancestor of *Cœloceras*, *Sphæroceras*, and *Stephanoceras*. Until the ontogeny of the genus is worked out, opinions on its phylogeny can not be much more than speculations.

The more remote derivation of the Ægoceratidæ is still more uncertain; Hyatt and nearly all other paleontologists regard *Psiloceras* as the radicle of the group, while many derive *Psiloceras* from the Phylloceratidæ, the development and phylogeny of which group have been very fully discussed by the writer in a recent paper (1898). In his opinion the ammonite radicle of this group is to be sought in *Nannites*, or in some Permian or Triassic genus of that transitional character. No attempt was made to trace the genealogy back into the goniatites, further than to indicate the probability that the remote radicle would be found among the Prolecanitidæ. The ontogeny of *Nannites* is still wholly unknown, but the writer has recently worked out the development of an undescribed genus, associated with, and evidently very closely related to *Nannites*, with larval and adolescent stages showing unmistakable glyphioceran affinities. F. Bernard (1895, p. 656) derives the Phylloceratidæ from *Popanoceras*, which is most improbable, in view of the evident derivation of that genus from the primitive Arcestidæ. E. Haug (1898, p. 45) traces the Phylloceratidæ through *Monophyllites* back to *Nomismoceras* and *Gephyroceras* of the phylum Gephyroceratidæ; although, as shown by the writer, the young stages of both *Phylloceras* and *Lytoceras* show an unmistakable resemblance to *Glyphioceras;* the ontogeny of *Nomismoceras* is unknown, so any attempt at present to trace its origin must be largely speculative; it may, however, have come from *Glyphioceras*.

Whatever the goniatite radicle of this group may have been, the secondary radicle of *Hoplites*, *Desmoceras*, *Ægoceras*, *Perisphinctes*, and *Cœloceras* was the same for all. The young stages of *Hoplites*, as figured by Branco (1879, Pl. XIII, fig. 2, *a–m*), resemble the young of Perisphinctes (Branco, 1879, Pl. XIII, figs, 1, *a–l*), while both resemble the larval and early adolescent stages of *Cœloceras*, as illustrated on Plate XII of Branco's memoir, and of *Desmoceras*

(Puzosia), on Plate XI, fig. 5, *a–k*. On Plate XIII, fig. 5, *a–n*, Branco has figured the early stages of *Cymbites*, which show all the essential characters observed in the larvæ of the other genera mentioned, although less accelerated, and necessarily more primitive.

The systematic position of *Hoplites*, according to the investigations of the writer, and of Sarasin (with whom the writer substantially agrees), is not with the Stephanoceratidæ, but with the Perisphinctinæ. *Desmoceras*, on the other hand, undoubtedly belongs to the Stephanoceratidæ, along with *Sonneratia*, for adolescent stages of both genera resemble perfectly *Stephanoceras*[1] and *Holcostephanus*, and these, in turn, sprang from *Cœloceras*. The ægoceran ancestor of *Cœloceras* and of the perisphinctoid group is the same, and can be traced back to a *Cymbites*-like form, and this must have originated in a genus with the essential characters of *Nannites*, with the possible intermedium of some primitive unknown member of the Phylloceratidæ. The immediate ancestor of *Hoplites* is not to be sought in a perfected *Cosmoceras*, nor did this genus spring from any highly specialized *Perisphinctes*, which, according to Buckman, is a degenerate group of the Stephanoceratidæ; nor was any fully differentiated ægoceran form the parent of this perisphinctoid ancestor. We must rather seek, in each case, the radicle in the primitive, unspecialized beginnings of each group. And if all these genera come from a phylloceran stock, they certainly do not come from *Psiloceras*, *Phylloceras*, nor *Lytoceras*, but from some primitive member of the Phylloceratidæ, as yet unknown, or at least not recognized as belonging to that group. At any rate, the stage between that resembling *Nannites*, and that suggesting *Cymbites*, is too short, and too little differentiated in any species of *Hoplites* yet investigated for a probable reference to *Monophyllites*.

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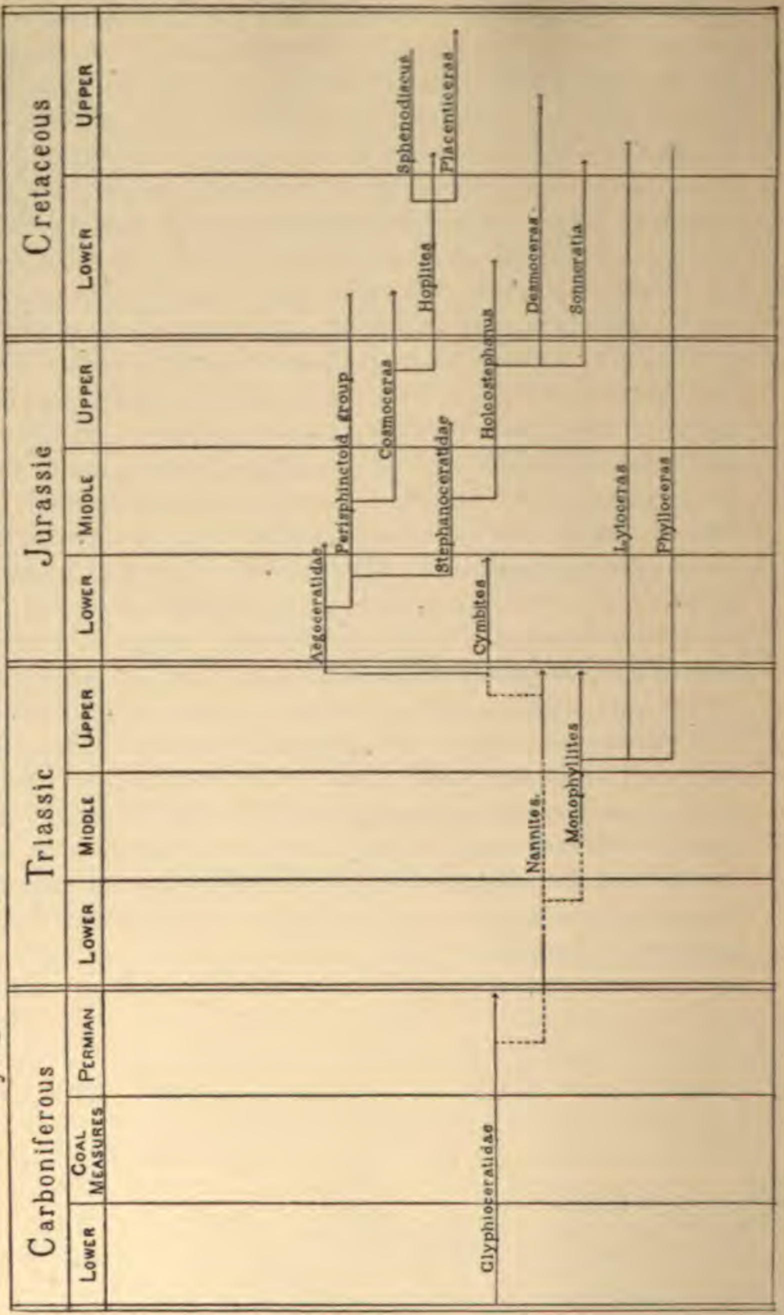
[1] The writer has recently worked out a remarkably perfect series of *Sonneratia stantoni* Anderson MS., *Desmoceras haydeni* Gabb, *D. breweri* Gabb, and *D. hoffmanni* Gabb, on which series the above statements are based.

As to the goniatite radicle of *Hoplites* and of the other perisphinctoids, the writer's investigations point to some glyphioceran form, possibly *Glyphioceras* itself. Now E. Haug (1898, pp. 39, 46, 73) claims that Hyatt's family, Glyphioceratidæ, is nothing but a group of morphological equivalents from three distinct stocks or *phyla*, the Glyphioceratidæ proper, the Gephyroceratidæ, and the Agoniatitidæ; a number of species grouped in this latter phylum are classed together under the new name *Pronannites*, as supposed ancestors of *Nannites*. Just this very group of glyphioceran forms most nearly resembles the goniatite stage of *Hoplites*. Haug is, then, in essential agreement with the writer, although he calls these by other names. Now since this classification of the goniatites, although certainly the best proposed up to this time, is too arbitrary, based too little on what we know, and too much on what may be so, the writer prefers for the present to call the goniatite stage of *Hoplites* glyphioceran, freely admitting that it may eventually be referred to *Pronannites*, or to some other genus at present insufficiently known. And should any of these stages be correlated with *Nomismoceras*, this genus should still, according to E. Holzapfel (1899), be referred not to the Gephyroceratidæ, but to the Glyphioceratidæ, the morphogeny of which group has already been described by the writer (Smith 1897). *Nomismoceras* is probably a derivative of *Glyphioceras*, for some species of *Lytoceras*, after passing through a glyphioceran stage, show what might be called a nomismoceran stage.

Phylogenic Table of Placenticeras and Associated Genera.



Placenticeras californicum *Anderson* (MS.).

PLATE XXV, FIGS. 1–8; PLATE XXVIII, FIG. 6.

Placenticeras californicum is most nearly related to *P. guadaloupæ* (Stoliczka, not Roemer), as described and figured by F. Stoliczka (1861), although it is more compressed laterally, and somewhat rougher shelled than the Indian species. The largest specimen found had the following dimensions:

	mm.
Diameter	120.00
Height of last coil	58.00
Height of last coil from the preceding	45.00
Width of last coil	30.50
Involution	13.00
Width of umbilicus	23.00

This specimen had about six revolutions, showed the body chamber to be about two-thirds of the last whorl, and since there was no further progressive development, seems to have been fully mature. The abdomen is narrow, flattened, with low central keel, and with marginal keels made up of a row of elongated knots. The sides are ornamented with rough sigmoidal ribs, branching out from coarse umbilical knots, and forming the knots on the abdominal shoulder keels.

Another specimen of five and a half revolutions was exactly like the larger one, and gave the following dimensions:—

	mm.
Diameter	77.00
Height of last coil	37.50
Height of last coil from the preceding	27.00
Width of last coil	20.00
Involution	10.50
Width of umbilicus	13.00

Horizon and Locality.—A single specimen of this species was found by Dr. L. G. Yates on the ranch of Mrs. Isabella Jordan, on the Arroyo del Vallé, Alameda county, California, about eight miles southeast of Livermore. Associated with it were found the following species: *Baculites chicoënsis* Trask; *Desmoceras hoffmanni* Gabb; *D. ? selwynianum* Whiteaves; *Hoplites remondi* Gabb; *Holcostephanus ? suciaënsis* Meek; *Lytoceras alamedense* Smith; *Lytoceras batesi* Trask; *L. (Tetragonites)* cf. *cola* Stoliczka; *L.* cf. *timotheanum* Mayor; *Placenticeras pacificum*, sp. nov., Smith; *Phylloceras onoënse* Stanton; *P. ramosum* Meek; *Cinulia obliqua* Gabb; *Inoceramus* cf. *vancouverensis* Shumard;

Trigonia evansana Meek; *Pectunculus veatchi* Gabb, and other species not identified, or not characteristic. This fauna is rather contradictory and puzzling, so that in a former paper (Smith, 1898, p. 138) the writer expressed the opinion that either the fossils from that locality, but from different beds, had not been differentiated in collecting, or that the strata were transitional from Horsetown to Chico. A visit in person to the locality, in the spring of 1899, enabled the writer to find out definitely that there was only one fossiliferous bed; and the identification of two species of *Placenticeras*, the young stages of which were formerly supposed by the writer to be *Hoplites*, place the Chico age, Cenomanian, of these beds almost beyond doubt. A still more certain determination of the age of this species is given by its occurrence, along with *P. pacificum* and a large number of typical Chico species, in the Chico beds one-half mile west of Henley, near Hornbrook, Siskiyou county, California, where it was discovered by Mr. Frank M. Anderson, to whose liberality the writer owes the use of all specimens of *P. californicum* from that locality figured in this paper.[1]

During the summer of 1899 Dr. Stephen Bowers, of Los Angeles, collected a number of Chico fossils in the San Fernando mountains, Los Angeles county; these were sent to the writer for inspection, and several specimens of *P. californicum* were found among them. From its wide range in northern, central, and southern California, always in the same horizon, it is fair to assume that *P. californicum* is characteristic of the lower Chico, or Cenomanian portion of the formation.

Poorly preserved young specimens of this species have a certain resemblance to *Schlœnbachia chicoënsis*, and have been occasionally mistaken for it; but the young stages of the two genera are so entirely different that a mistake is hardly possible if one examines the inner coils.

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[1] In the Proceedings of the California Academy of Sciences, 3d Series, Mr. Anderson will describe this fauna in his monograph on the Cretaceous, and with his permission the writer uses his manuscript name "*Placenticeras californicum* Anderson."

LARVAL AND ADOLESCENT STAGES.

The earliest stages of *Placenticeras californicum* could not be observed on the specimens at hand. The smallest specimen obtained, figured on Pl. XXV, figs. 1 and 2, was in the perisphinctoid stage, and very like the corresponding stage of *Placenticeras pacificum*, except that the shell is a little rougher, and somewhat more evolute than on that species; it consisted of two and three-eighths coils, and had the following dimensions:—

	mm.
Diameter	3.32
Height of last coil	1.44
Height of last coil from the preceding	1.11
Width of last coil	1.33
Involution	0.33
Width of umbilicus	1.16

At about two and a quarter coils the constrictions cease, the ribs end in knots on the abdominal shoulders, and the cosmoceran stage begins at diameter of about four millimetres, just as in *P. pacificum*, but the sculpture is rougher, and the shell more robust. At about three coils and diameter of eight millimetres the sculpture and shape of the shell resemble strongly *Hoplites tuberculatus* Sowerby, of the Gault; this specimen, figured on Pl. XXV, fig. 3, gave the following dimensions:—

	mm.
Diameter	8.00
Height of last coil	4.10
Height of last coil from the preceding	2.80
Width of last coil	3.30
Involution	1.30
Width of umbilicus	1.80

At three and five-eighths coils, diameter 14 mm., the resemblance to the group of *Hoplites interruptus* has become so striking that the young shell might well be taken for an adult of that group, were it not for the fact that this entire group of *Hoplites* was either extinct at this time, or at least had changed entirely into other genera. This specimen is figured on Pl. XXV, figs. 4 and 5, to illustrate the most typical *Hoplites* stage of growth of the species, and to show the striking difference between *P. californicum* and *P. pacificum* at this stage. Both correspond to *Hoplites*, and both to the group of *H. interruptus*, but the late adolescent stage of *P. pacificum* corresponds closely to *H. splendens*, while *P. californicum* corresponds to the rougher and more evolute species, and retains many cosmoceran characters lacking in the other form.

As the adolescent period advances the resemblance to *Hoplites dufrenoyi* d'Orbigny, of the Gault of Europe, becomes marked, although *P. californicum* differs from the European species in having the ribs finer, more numerous, more sharply bent on the sides, and in having the rows of knots on the abdominal shoulder keels closer together, and weaker. There is also a rather faint second row of knots high up on the sides, where the ribs fork at the sharp forward bend; this is a cosmoceran character lacking on *H. dufrenoyi*. The ribs start out in pairs from a knot on the umbilicus, and between each pair there is usually a single rib intercalated. The rows of knots on the umbilicus, on the sides, and on the abdominal shoulders, are stronger at diameter of fifteen millimetres than at maturity, showing this to have been characteristic of the immediate ancestor of the genus. The relative measurements agree exactly with *H. dufrenoyi*, except that on the Californian species the whorl is broader, and the cross-section polygonal.

The adolescent stage of *P. californicum*, Pl. XXV, figs. 6 and 7, at about four coils, gave the following dimensions:—

	mm.	
Diameter	22.00	1.00
Height of last whorl	10.50	0.48
Height of last whorl from the preceding	8.25	0.37
Width of last whorl	8.00	0.36
Involution	2.75	0.11
Width of umbilicus	6.30	0.28

Compare with these the almost identical measurements of *H. dufrenoyi*, at the same stage of growth:—

	mm.	
Diameter	21.50	1.00
Height of last whorl	10.00	0.47
Height of last whorl from the preceding	7.50	0.35
Width of last whorl	6.50	0.30
Involution	2.75	0.11
Width of umbilicus	6.00	0.28

On the fifth whorl the likeness to *Hoplites* becomes less, and the characters of *Placenticeras* more strongly accentuated; the central abdominal keel stands up almost as high as those on the shoulders, while the sigmoidal ribs are no longer so sharp as in the earlier adolescent stages. This may be considered as the transition to maturity, although the *Hoplites* characters do not disappear at once, nor do the *Placenticeras* characters appear all at the same time; some, in fact, show even at the beginning of the adolescent stage. A specimen illustrating the transition is figured on Pl. XXV, fig. 8; it consists of four and a half coils, and gave the following dimensions:—

	mm.
Diameter	34.50
Height of last coil	18.00
Height of last coil from the preceding	13.00
Width of last coil	9.50
Involution	5.00
Width of umbilicus	5.00

P. californicum might easily be confused with *P. guadaloupæ* Stoliczka (1861) (not Roemer), of the Trichinopoly group, Upper Cretaceous[1], but differs from it in being more compressed laterally, in having rougher sculpture, and in lacking the heavy nodes on the sides below the abdominal shoulders. The two species may be identical, but until we know the limits of variation of them, it would be unsafe to class them together.

Placenticeras pacificum, sp. nov.

Plate XXIV, Figs. 1–21; Plate XXV, Figs. 9–11; Plate XXVI; Plate XXVII, Figs. 1–13; Plate XXVIII, Figs. 1–5.

Placenticeras pacificum is large, discoidal, involute, and laterally compressed, having the typical plate shape of the genus. At maturity the whorl embraces somewhat more than one-half of the preceding; the breadth of the whorl is one-fifth of the diameter, the height of the whorl is three-sevenths, and the width of the umbilicus one-fifth. The body-chamber is about two-thirds of a revolution in length. The abdomen is narrow, flattened, slightly concave, bounded by a row of elongated knots forming rough keels. Up to diameter of about one hundred millimetres, five and a half coils, the shoulder keels are rather finely notched by the ends of the lateral ribs; at this stage the coarse elongated knots of *Placenticeras* appear, and deep undulations cross the abdomen; a central keel, which has persisted up to this stage, becomes obsolete. The sides are ornamented with rather coarse sigmoidal ribs, bundling on umbilical knots; these show on the cast even more strongly than on the shell. The outer shell has numerous sigmoidal striæ covering the ribs and the interspaces. The umbilicus is moderately narrow, and the shoulders angular, becoming more so as age advances. At five and two-thirds coils the umbilicus is one-sixth of the diameter, while at six and one-third coils it widens out to one-fifth, this change probably indicating old age, for the slackening of the increase of height of the body-chamber shows a decrease in growth force.

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[1] Stoliczka's species is probably not identical with Roemer's *P. guadaloupæ*, from the Lower Cretaceous of Texas, zone of *Mortoniceras rostratum*.

The septa consist of an abdominal lobe with a pair of long branches, and seven lateral lobes, all finely digitate, and rather narrow. The saddles are broader and deeply divided by narrow secondary lobes.

Douvillé (1890, p. 288) says that in *Placenticeras* the first, second, and third lateral lobes are probably formed out of divisions of a primary lobe, and that the fourth is really the second primary. But the development of this species shows that the first lateral lobe is developed out of a division of the primary lateral saddle, and that the second, third and fourth lobes are developed out of notches in the primitive first lateral lobe. There are also three auxiliary lobes on the sides, and one on the umbilical shoulders, growing simpler as the umbilicus is approached. This is a common and well known fact, ascribed by Jackson (1899) to the principle of localization of stages of growth, by which more primitive characters are preserved in the dorsal and umbilical portion of the shell. At early maturity these lobes are arranged in a wide backward-pointing curve, but in later growth this curve is not nearly so pronounced. The development of the septa, as shown in the adolescent stages, makes it clear that the three chief lateral lobes are merely modifications out of the three points of the triænidian primitive lateral lobe. This explains the arrangement in a curve, and also the straightening out of this curve as full maturity is approached. This suggests a probable explanation for the large number of lobes found in many ammonites, such as *Placenticeras* and *Sphenodiscus*, although it is not yet known that the development of the latter genus takes place in this way. The arrangement of the lobes in

Placenticeras guadaloupæ Roemer (Pl. XXVIII, fig. 8) suggests this origin for part of them. It is commonly accepted that in the ammonites new elements in the septa develop on the dorsal side near the umbilicus, and appear on the outside only in later growth; here in the development of *Placenticeras* this is decidedly not the case, for the three principal lobes are developed out of one that was on the outside from the very beginning.

Placenticeras pacificum is most nearly akin to *P. californicum*, with which it agrees in the width of the umbilicus, but from which it differs in the more compressed whorl, more numerous, finer ribs, and the smaller size of the knots on the umbilicus. In *P. pacificum* the breadth of the last whorl is one-fifth of the diameter, and in *P. californicum* it is one-fourth, but in the young stages the relative measurements of the two species are very much the same, although there is no danger of confusing them above the diameter of four millimetres. *P. pacificum* might also be compared with *P. guadaloupæ* Stoliczka (1861) (not Roemer), but the Indian species is even thicker than *P. californicum*, and has a row of coarse knots on the umbilical shoulders, and another near the abdominal shoulders, which would distinguish it from either Californian shell. Also, the ribs on the Indian species do not show that strong sigmoidal bend seen on the others.

Horizon and Locality.—Placenticeras pacificum was first found by Dr. L. G. Yates on the Arroyo del Vallé, ranch of Mrs. Isabella Jordan, Alameda county, California, about eight miles southeast of Livermore. Associated with it were found the following species: *Baculites chicoënsis* Trask; *Desmoceras hoffmanni* Gabb; *D. ? selwynianum* Whiteaves; *Hoplites remondi* Gabb; *Holcostephanus ? suciænsis* Meek; *Lytoceras alamedense* Smith; *Lytoceras batesi* Trask; *L.* cf. *cola* Stoliczka; *L.* cf. *timotheanum* Mayor; *Placenticeras californicum* Anderson (MS.); *Phylloceras onoënse* Stanton; *P. ramosum* Meek; *Cinulia obliqua* Gabb; *Inoceramus* cf. *vancouverensis* Shumard; *Pectunculus veatchi* Gabb; *Trigonia evansana* Meek; *Nucula truncata* Gabb, and other species not especially characteristic. This fauna almost undoubtedly indicates the lower part of the Chico formation Cenomanian, Upper Cretaceous.

P. pacificum was afterwards found by Mr. F. M. Anderson one-half mile west of Henley, near Hornbrook, Siskiyou county, California, associated with *P. californicum*, *Pachydiscus newberryanus* Meek, *Phylloceras ramosum* Meek, *Hoplites* cf. *remondi* Gabb, *Chione varians* Gabb, *Mactra ashburneri* Gabb, *Cinulia obliqua* Gabb, *Cylichna costata* Gabb, and a number of other characteristic Chico species; from this locality came the type of the species, figured on Pl. XXVI. Mr. F. Rolfe has recently found this species in the lower Chico beds of the canyon of Silverado creek, near the old coal mine, about two miles east of the mouth of the canyon, where Silverado empties into Santiago creek.

Placenticeras pacificum, since it occurs in the same horizon in northern, middle and southern California, may be taken as characteristic of the lower Chico; so the reference of the beds to the Horsetown, made by the writer (Smith, 1898) in a former paper, will have to be revised, for a careful study has shown the accompanying faunas at all three localities to be characteristic of the Chico, and not of the Horsetown.

LARVAL STAGES.[1]

Phylembryonic Stage.—The young *Placenticeras* was undoubtedly shelled before it was hatched, although it was not possible, on the specimens under investigation, to find out certainly the limits of the primitive embryonic body-chamber; but this seems to have coincided approximately with the limits of the protoconch, although it may have included somewhat more of the spiral coil. Branco (1879, p. 24), on the other hand, is of the opinion that the embryonic shell could not have taken up the entire protoconch, but must have been homologous with the primitive cap-shaped shell of the gastropods, and only in later growth was the spiral formed. It has, however, been shown by Dr. Amos Brown (1892) that in *Baculites* the limits of the embryo chamber lie between the first and second septa. This has also been observed by the writer on the young of *Baculites chicoënsis*, and on *Lytoceras alamedense*.

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[1] In the nomenclature of stages of growth the writer has followed Hyatt's "Phylogeny of an Acquired Characteristic."

The protoconch of *Placenticeras pacificum* (Pl. XXIV, figs. 1–3) has diameter 0.54 mm., and width 0.75 mm.; it is smooth, oval, and covered by the primitive nacreous shell, which extends to the end of the first coil. This protoconch is very similar in all the later ammonites, and is probably an adaptive form, due to life in the egg, and does not represent any ancient ancestral genus, for none of the early cephalopods were shaped like this. It is, then, the typical embryo of the ammonoids, and yet can hardly be said to be correlative with any group of cephalopods.

Ananepionic.—With the formation of the first septum the young ammonite has taken its place among the chambered cephalopods, and has become, for the time being, a nautiloid, although it is not possible, from the exceedingly simple nature of the shell, to correlate it with any especial genus. Nor, indeed, is it strictly homologous with any ancient nautilian form, for the larval ammonite even in its first stages possesses several elements unknown in that group. The first septum, which separates the larval body-chamber from the embryonic shell, is nautilian in character, but the siphuncle begins inside the protoconch with a siphonal knob, or cæcum, and the protoconch itself is calcareous. These are two characters that the nautiloids, even to this day, have never yet acquired. It would, then, be impossible to correlate the ananepionic stage with any ancestral genus, since we have in this stage ammonoid characters pushed back by unequal acceleration, until they occur contemporaneously with more remote ancestral characters. This stage and these characters can not correctly be called adaptive, for they are undoubtedly hereditary, although not inherited at equal rates.

The ananepionic septum (Pl. XXVII, fig. 1) consists of a narrow, undivided, abdominal saddle, and a short lateral saddle; the internal portion of the septum is gently curved, and gives little indication of the lobes and saddles that appear on the second chamber-wall. The only part of the shell that can with certainty be assigned to the ananepionic period of growth is that lying between the first and second septa, but that is probably not all of this second living chamber. The outer nacreous shell is smooth and devoid of all ornament until the end of the first coil, hence it seems likely that the ananepionic body-chamber extended throughout this coil, the end of which is marked by a distinct constriction, and beginning of sculpture, as seen on Pl. XXIV, figs. 3–9. While this portion of the shell became chambered in later larval stages, it was a spiral unchambered coil during the first free stage of the animal. This is true not only of this species of *Placenticeras*, but also of the early larval stages of every ammonite yet seen by the writer, embracing typical genera from the Carboniferous, Trias, Jura, and Cretaceous, retrogressive and progressive forms alike.

Metanepionic.—Following the usage of Hyatt, the middle larval stage is considered to have begun when the shell has assumed ammonoid characters; this happens with the formation of the second septum, and continues as long as only simple goniatite characters are seen. In the older ammonoids the second septum always has an undivided ventral lobe distinctive of the Nautilinidæ and their immediate descendants; but in the later and more specialized ammonites the second septum already has the ventral lobe divided by a siphonal saddle, so that the record of the Nautilinidæ is lost from the shell. The metanepionic stage is shown on Pl. XXIV, figs. 3–7, and its septa on Pl. XXVII, fig. 2. The divided ventral lobe, the lateral lobe and that on the umbilical shoulder, along with the broad low whorl and smooth shell, all remind one strongly of *Glyphioceras*, a genus diagnostic of the Carboniferous; because of this resemblance, and because some member of the Glyphioceratidæ may probably have been the ancestor of *Hoplites*, this stage is called glyphioceran, although *Pronannites*, or several other genera excluded from this family by some writers, may have been the parent group. In all probability this stage is prosiphonate, although the siphonal collars could not be seen on any specimen, for the higher members of the Glyphioceratidæ become prosiphonate with advancing age, and many of the Cretaceous ammonites investigated become prosiphonate almost as soon as they reach the goniatite stage of development.

At about one-quarter of the first revolution from the protoconch, and at the fourth chamber-wall, a second internal lateral lobe is added, something that no member of the Glyphioceratidæ is known to have possessed;[1] this stage is distinctly goniatitic, and yet not comparable to any known genus, but is probably the result of unequal acceleration of the septation, introducing elements that belonged to later genera. This is shown on Pl. XXVII, fig. 2, and illustrates the multiplication of the lobes by the division of those inside the umbilicus, and gradual pushing of these towards the ventral portion of the shell.

Paranepionic.—At about five-eighths of a coil the new internal lobe reaches the umbilical border, and the shell then has two principal lateral lobes and one auxiliary. The larva has then reached a stage correlative with the goniatites of the Upper Carboniferous. This period of growth did not last long, for shortly after the appearance of the constriction which marks the end of the first coil the septa lose their goniatitic character and become transitional to the ammonite stage. This is shown on Pl. XXVII, figs. 3 and 4, and the outside form of the shell on Pl. XXIV, figs. 6 and 7. At one and one-twelfth coils the shell is transitional from the glyphioceran stage (*Pronannites*) to what resembles closely the genus *Nannites* of the Trias, as shown on Pl. XXIV, figs. 8 and 9; the dimensions at this stage were as follows:—

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[1] Haug, "Études sur les Goniatites", p. 27, fig. 6, *e*, shows *Pericyclus* with two internal lateral lobes, but this was wrongly copied from Holzapfel's original drawing, "Carbon-Kalke von Erdbach", Pl. III, fig. 6, where only one internal lateral lobe is shown.

	mm.
Diameter	1.32
Height of last whorl	0.57
Height of last whorl from the preceding	0.41
Width of last whorl	0.90
Involution	0.16
Width of umbilicus	0.58

If it had not been said that this was a minute young shell taken out of an older individual, any paleontologist would refer it without hesitation to the Glyphioceratidæ, and probably to that group designated by Haug (1898, p. 40) as *Pronannites*, of the Lower Carboniferous; the only character in which it differs from that group is in the two internal lateral lobes, and this, in the opinion of the writer, is the result of unequal acceleration, causing the introduction into the glyphioceran stage of elements that belonged to the descendants of this group. Moreover, there must have been some adult form with this character, for *Paralegoceras* has three external lateral lobes, and must have developed out of a form with glyphioceran or gastrioceran shape and the supernumerary internal lobes, since the new elements usually develop inside the umbilicus. This stage ends at one and one-fourth coils, diameter 1.50 mm., having lasted about one-half a revolution.

Adolescent Stages.

Ananeanic—Cymbites Stage.—When the young animal has taken on characters that, if occurring in an adult, would stamp it as an ammonite and not a goniatite, it may be considered as adolescent; by this it is not meant to imply that there is any sharp line of demarcation between these two groups, for there are a number of genera that might, with equal propriety, be classed in either division; it is admitted, too, that this manner of subdividing ontogenic stages is artificial, and that it would be much more satisfactory merely to call a stage by the name of the genus with which it is correlated, if we could only be sure of this correlation. But, on account of unequal acceleration, and obscure development of characters in young ammonites, it is usually impossible to correlate them with certainty with any particular ancestral genus. And this difficulty increases when we leave the larval stages, and are concerned with later growth.

The ananeanic stage begins at one and a-quarter coils, diameter 1.50 mm., when the pointed lateral lobe develops round prolongations on each side and becomes trifid (triænidian); about the same time the lateral saddle becomes indented, showing the first indication of digitation of the septa. Sculpture appears on the shell here for the first time, at first apparently merely a repetition of the constrictions and varices that began at the end of the first coil, then developing faint but distinct ribs between the constrictions. The septa at this stage are shown on Pl. XXVII, fig. 5, one and three-eighths coils, and of the following dimensions:—

	mm.
Diameter	1.70
Height of last whorl	0.76
Height of last coil from the preceding	0.61
Width of last coil	0.95
Involution	0.15
Width of umbilicus	0.68

This first adolescent stage resembles greatly *Cymbites*, *Diaphorites*, and *Pimelites*, any one or all of which may well have been ancestors of the ægoceran stock, although it is impossible to speak with certainty or even probability, especially since the relations of these genera to each other are, as yet, only conjectural; the writer agrees with Buckman (1898), who regards *Cymbites* as the radicle of the ægoceran stock, but makes no mention of the other genera. This stage will be referred to as the *Cymbites* stage.

On Pl. XXIV, figs. 10 and 11, is figured a specimen of *P. pacificum* in the *Cymbites* stage, one and seven-twelfths coils and of the following dimensions:—

	mm.
Diameter	1.99
Height of last coil	0.78
Height of last coil from the preceding	0.66
Width of last coil	0.96
Involution	0.12
Width of umbilicus	0.75

Hyatt (1889) thought that Neumayr's genus was founded on immature specimens, probably of the genus *Agassizceras*, while Haug does not think that the characters upon which the genus was based are sufficiently constant to warrant the separation. But whether *Cymbites* is a valid genus or not, there must have been such a form in the ancestral line of the Ægoceratidæ, and thus of *Hoplites* and *Placenticeras*. So the name will be used until the genus is given a name that will stand, in case the old designation is thrown out.

Cymbites has been found only in the Lower Jura, but from its character must have occurred also in the Trias, for it is simpler in septa than any other ammonite of the Jura. This stage lasts in *Placenticeras* about three-eighths of a coil and ends at diameter 2.20 mm., one and five-eighths of a coil from the protoconch.

Ægoceran Stage.—With the beginning of this part of the adolescent stage the division of the lateral lobe becomes more pronounced, and a secondary indentation begins on the side away from the abdomen. The whorl grows higher, and the rounded exterior gives place to somewhat flattened sides with abdominal shoulders. The sculpture becomes stronger, and the shell is already decidedly ægoceran in appearance. The specimen figured on Pl. XXIV, figs. 12 and 13, and the septa on Pl. XXVII, figs. 6–8, show three internal lateral lobes, an advance in development that is more forward than that of *Hoplites dufrenoyi* at diameter 5.00 mm. At one and seven-eighths coils the young ammonite gave the following dimensions (Pl. XXIV, figs. 12 and 13):—

	mm.
Diameter	2.64
Height of last whorl	1.19
Height of last whorl from the preceding	0.98
Width of last coil	1.16
Involution	0.21
Width of umbilicus	0.80

Perisphinctoid Stage.—At two revolutions, diameter 3.00 mm., the sides become still more flattened and the abdominal shoulders squarer, giving a perisphinctoid aspect, heightened by the frequent varices and the strong intermediate ribs on the sides and abdomen. It should be noted that the development of the septa has not kept pace with the other characters, for in small adolescent stages of ammonites, on account of their minute size and the thickness of the shell, it is physically impossible for the septa to have the complexity of the corresponding adult genus. Another reason is that the retardation in development of the septa, which is distinctive of *Placenticeras*, begins to show itself here. This retardation becomes more pronounced as the stages advance, so that it becomes more than mere unequal acceleration of characters, for in the septa the *Hoplites* stage of development is never reached, the differentiation of the first lateral lobe into three secondary lobes being already complete. This differentiation shows itself quite distinctly in the perisphinctoid stage. The other characters are not affected by retardation to nearly so great an extent as the septa, or it may be more correct to state that retardation can not be detected in the other characters.

A specimen of two and a-quarter coils, figured on Pl. XXIV, figs. 14 and 15, gave the following dimensions:—

	mm.
Diameter	3.50
Height of last whorl	1.63
Height of last whorl from the preceding	1.36
Width of last whorl	1.40
Involution	0.27
Width of umbilicus	1.06

In everything but the comparative simplicity of the septa this stage is distinctively perisphinctoid, but cannot be correlated with any particular genus of that group, especially in view of the fact that according to the researches of Buckman, quoted above, *Perisphinctes* itself is a degenerate of the stock of the Stephanoceratidæ. The perisphinctoid stage lasts up to two and a-quarter coils, diameter about 3.50 mm.

Metaneanic—Cosmoceras Stage.—In this stage the ribs no longer cross the abdomen, but end in tubercles on the abdominal shoulders, forming well defined shoulder keels, with a furrow between them. The varices and constrictions cease abruptly with the beginning of the stage, at about two and a-quarter coils. The ribs become faint on the sides, but are strong on the umbilicus and on the shoulders, giving a strong resemblance to *Cosmoceras*, which increases as the stage advances. The septa at first are comparatively simple, although ammonitic. The first lateral lobe begins to lose its identity as a separate lobe, the three divisions of this becoming independent. The outside indentation of the external saddle also begins to assume the proportions of an independent lobe. At the beginning of the stage there are four external primary lateral lobes, and three internal; but about the middle of the third coil, diameter 4.50 mm., the indentation of the external saddle, and the three divisions of the large primary lateral lobe assume the proportions of independent lobes, their arrangement in a curve showing their secondary nature. This is shown on Pl. XXVII, figs. 10–13, where the septa are seen to be remarkably like those of *Diaphorites* Fucini, (Pl. XXVIII, fig. 7), although the shell has long since passed through the stage resembling *Diaphorites*. This is a rather unusual way for new elements to be added to the septa, they usually coming in at the umbilicus. As a consequence of this mode of addition the complexity does not decrease from the abdomen towards the umbilicus, but decreases both ways from the middle of the sides. It would be hard for one that had seen only the adult to believe that the first four lateral lobes had been developed out of one primary lobe. A somewhat similar development has been observed by the writer in the Pinacoceratidæ.

While the almost smooth sides, the strong abdominal shoulder keels made up by growing together of tubercles at the outer ends of the ribs, the narrow umbilicus, and the high narrow whorl all show affinities with *Cosmoceras*, the septa never reach, during this stage, the complexity of that genus. This may be due either to the greater acceleration of development of the form and ornamentation of the shell, or to the physical impossibility of having a chamber-wall take on so many convolutions at the edge in so small a space. Most probably the former explanation is the correct one. A specimen of this stage is figured on

Pl. XXIV, figs. 16 and 17, two and three-eighths coils, and of the following dimensions:—

	mm.
Diameter	4.10
Height of last whorl	1.83
Height of last whorl from the preceding	1.55
Width of last whorl	1.70
Involution	0.28
Width of umbilicus	1.16

On this specimen the *Nannites* stage was seen on the second coil, the perisphinctoid stage on the third coil up to diameter 3.60 mm., two and a quarter coils, while the cosmoceran stage begins just after the last constriction visible on the shell, and lasts up to the end of the third coil, diameter about 7 mm. In this stage the shell resembles a species included by some paleontologists in the genus *Oppelia*, *Ammonites bipartitus* Zieten, as figured by Quenstedt in "Ammoniten des Schwäbischen Jura", Pl. LXXXV; but Quenstedt included that species under the *Ornati*, and evidently considered it as a *Cosmoceras*.

A larger specimen in the *Cosmoceras* stage is figured on Pl. XXIV, figs. 18, 19, showing the distinct bundling of the ribs on the sides, and the coarse abdominal tubercles; this specimen at two and five-sixths coils showed the following dimensions:—

	mm.
Diameter	6.60
Height of last coil	3.15
Height of last coil from the preceding	2.40
Width of last coil	2.07
Involution	0.75
Width of umbilicus	1.46

On this specimen the body-chamber occupied two-thirds of the last coil, and was incomplete even then; the last half coil was taken up by the cosmoceran stage, and the first half by the ægoceran and the perisphinctoid stages.

Just how long the cosmoceran stage lasts or when it ends it is impossible to say, because the change into the next stage is so gradual, and because it comes at such different sizes on different individuals. Since the characters of any one generic stage do not appear or disappear all at once, on account of unequal acceleration of development of these characters, no one stage is exactly correlative with any particular genus. Thus in naming the stages after genera, it is merely meant that the characters of those genera are predominant. This effect of unequal acceleration becomes more marked as the adolescent stage advances. Near the end of this stage appears the central abdominal keel of *Placenticeras*.

Paraneanic—Hoplites Stage.—Near the beginning of the fourth coil, diameter slightly over 8 mm., the ribs are reduced to mere faint undulations and fine sickle-shaped striæ on the sides and umbilicus, while the external tubercles become almost obsolete, forming mere notches on the continuous abdominal keels. Specific characters begin to appear here, and there is no longer any doubt as to the family to which it belongs; this may be considered as the beginning of the *Hoplites* stage. The septa have not yet reached the complete development of the genus, although on Pl. XXVIII, figs. 1 and 2, a considerable advance over the *Cosmoceras* stage may be seen, especially in the digitation of the secondary lobes. A perfect specimen of three and a half coils, figured on Pl. XXIV, figs. 20 and 21, showed the transition from the cosmoceran to the *Hoplites* stage, and gave the following dimensions:—

	mm.
Diameter	12.00
Height of last whorl	7.00
Height of last whorl from the preceding	5.50
Width of last whorl	3.60
Involution	1.50
Width of umbilicus	2.00

With this stage begin the umbilical knots, which persist and grow stronger, being characteristic of the mature *Placenticeras;* the sculpture becomes fainter, and the tubercles on the shoulder keels subside into faint notches; at the same time the lateral compression becomes more pronounced, and the shell becomes discoidal and very high-whorled. *Placenticeras pacificum* at this stage is wholly unlike *P. californicum*, with which it is associated, being much more compressed and discoidal, with narrower abdomen, flatter sides, much less distinct sculpture, and narrower umbilicus, although in the earlier adolescent periods both species are very much alike. This stage of growth is most nearly related to *Hoplites splendens* of the Gault, Lower Cretaceous, of Europe, but differs from it in being more compressed laterally, in the narrower abdomen, and the smoother abdominal keels, which on *H. splendens* have a row of tubercles like the adolescent stage of *Placenticeras pacificum*. The septa of the European species differ considerably from those of the Californian, showing none of the degeneration in the approach to *Placenticeras*, which genus, according to Douvillé (1890, p. 290), is a descendant of *Hoplites*.

In the adolescent stage the four secondary lobes, formed from the first lateral by subdivision, swing more and more out of the original curve, and finally in maturity all semblance of the original lobe is lost. The septa then begin to bear some resemblance to *Placenticeras*, as does also the shape of the whorl, and the lack of marked sculpture of the shell. This species is now evidently on the road to becoming a *Placenticeras*, although it has not yet reached that stage of development; this seems to confirm the conjecture of Douvillé as to the origin of that genus, which was formerly classed with the Amaltheidæ.

EPHEBIC OR ADULT STAGE.

When the septa have reached the characters of *Placenticeras*, and undergo no further generic development, the adult stage may be said to have begun. But these characters begin singly, so there is no sudden transition from *Hoplites* to *Placenticeras*. Retardation in development of the septa shows itself early in the adolescent period, and grows more marked as the stage advances, so that the full generic development of *Hoplites* is never reached. At the diameter of 15 mm. the septa have already attained the development of *Placenticeras*, while the shell is decidedly a *Hoplites*. But when the shell becomes extremely discoidal, the umbilical knots strong, the lateral sculpture weak, and the central and marginal ventral keels a decided feature, the shell is no longer comparable to any species of *Hoplites*, even though many characters of that genus still remain. This may be called the transition to *Placenticeras*.

A specimen with the transition just beginning is figured on Pl. XXV, figs. 9 and 10, four coils, and diameter 20.5 mm., showing the fine sculpture, sharp, slightly notched marginal keels, and narrow umbilicus with faint nodes. A cross-section of this stage is shown on Pl. XXVIII, fig. 5. This stage continues unchanged to four and five-eighths coils, diameter of about 38 mm., where the ribs become suddenly coarse, and undulating nodes begin to show on the marginal keels. A specimen of this stage is figured on Pl. XXV, fig. 11, showing the sudden transition from fine to coarse sculpture. Now, for the first time, this species can certainly be placed among the typical members of *Placenticeras*, as defined by Meek, so the transition period is over, and the animal is really mature in characters, although not yet in size, since it grows nearly five times as large, and adds many more specific characters. This stage continues unchanged for nearly a revolution, the septa growing somewhat more complex, but advancing little beyond those seen at diameter of 15 mm. The septa, at the latest stage where they were visible, five and a-third coils, are shown on Pl. XXVIII, fig. 4. The septa of *P. guadaloupæ* Roemer, copied on Pl. XXVIII, fig. 8, show a decided resemblance to those of *P. pacificum*, but are more finely digitate, and have two more auxiliary lobes; but the arrangement of the three principal lateral lobes in a backward-pointing curve is suggestive of a similar secondary origin. *Placenticeras placenta* Dekay has departed still further from the parent type and has its lobes arranged almost in a straight line, and this character is pushed back by acceleration of development until it is seen even in the larval stages, as shown by Jackson (1899, Pl. XXV, figs. 118 and 119). The early larval stages were not figured, so it is not possible to be sure that the lateral lobes developed by subdivision, but this is very probably the case.

In extreme maturity the central abdominal keel becomes obsolete, and the fine notches on the marginal keels are transformed into rough elongated nodes; the ribs become coarser, with deeper furrows separating them, crossing even the flattened abdomen. The species now begins to have considerable resemblance to *P. placenta*, although not more than every member of a genus ought to show to the type, but it never departs so far from the *Hoplites* group as does *P. placenta*. The characters of extreme maturity begin at about five and two-thirds coils, diameter 118 mm; how long they lasted, or whether there was any further change it is impossible to say, as the largest specimen seen had diameter 172 mm., and still showed no senile degeneration, unless the widening of the umbilicus is due to deficiency of growth force. This specimen is the type of the species (Pl. XXVI); it is the property of Mr. F. M. Anderson, of Yreka, California.

The genus *Sphenodiscus* was included by Meek as a subgenus under *Placenticeras*, and has been considered by Douvillé as having a common origin with that group in *Hoplites;* both genera seem to have had their origin during the upper part of the Lower Cretaceous, but *Sphenodiscus* does not seem to have been either ancestor or descendant of *Placenticeras*, and, therefore, cannot be considered as a subgenus under it.

Placenticeras shows retardation and degeneration, but *Sphenodiscus* has departed still further from the parent type; its secondary lobes have swung more nearly into a straight line, and have become simpler, by retardation, until they are almost ceratitic in character. But this simplification of the septa can not be referred to reversion to any ancestral characters, since they were never present in any of its ancestors. The ontogeny of this genus is unknown, but it will probably show the larval and earliest adolescent stages normal in number and character of lobes, and with this subdivision into secondary lobes pushed by acceleration of development to an early stage. The life-history of *Sphenodiscus* would then repeat a part of the ontogeny of *Hoplites*, but can not give the complete record.

TABLE OF CROSS-SECTION OF PLACENTICERAS PACIFICUM.

	Phylembryonic.	*Glyphioceran Metanepionic.*	*Nannites Paranepionic.*	*Cymbites Ananeanic.*	*Ægoceran Ananeanic.*	*Cosmoceran Metaneanic.*	*Hoplites Stage Paraneanic.*		
	Proto-conch.	½ coil.	1 coil.	1½ cls.	2 coils.	2½ cls.	3 coils.	3½ coils.	4 coils.
	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
Diameter	0.61	0.88	1.21	1.79	2.65	4.22	7.00	12.00	20.75
Height of last whorl	....	0.48	0.49	0.64	0.98	1.95	3.48	6.20	11.00
Height of last whorl from the preceding	....	0.27	0.33	0.58	0.86	1.57	2.82	5.00	8.70
Width of last whorl	0.80	0.94	0.89	0.91	1.11	1.49	1.99	3.15	5.25
Involution	....	0.21	0.16	0.06	0.12	0.38	0.66	2.20	2.50
Width of umbilicus	....	....	0.12	0.58	0.91	1.24	1.58	2.50	4.00

TABLE OF STAGES OF GROWTH OF PLACENTICERAS PACIFICUM.

						Sculpture begins.	Lobes become ammonitic.
	Phylembryonic.	*Ana- to Metanepionic.*		*Paranepionic.*			
	Nautilian.	*Glyphioceran.*		*Transition to Nannites.*		*Nannites.*	
	Proto-conch.	P. and ⅓ coil.	P. and ½ coil.	P. and ¾ coil.	1 coil.	1 1/12 coils.	1¼ coils.
	mm.	mm.	mm.	mm.	mm.	mm.	mm.
Diameter	0.54	0.76	0.83	0.98	1.16	1.32	1.57
Height of last coil	.....	0.41	0.34	0.33	0.38	0.57	0.65
Height of last coil from the preceding	.....	0.28	0.25	0.25	0.32	0.41	0.53
Width of last coil	0.75	0.86	0.80	0.80	0.72	0.90	0.90
Involution	.....	0.13	0.09	0.08	0.06	0.16	0.12
Width of umbilicus	....	.....	0.26	0.23	0.46	0.58	0.61

	Distinct ribs begin.	First lateral lobe becomes trifid.			Whorl becomes helmet-shaped.		Sides and abdomen flatten, and the shoulders become distinct.	
	Ananeanic.							
	Cymbites.				*Ægoceran.*		*Perisphinctoid.*	
	1⅜ coils.	1½ coils.	1 7/12 coils.	1⅔ coils.	1¾ coils.	1⅞ coils.	2 coils.	2¼ coils.
	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
Diameter	1.70	1.82	1.99	2.20	2.40	2.64	2.82	3.50
Height of last coil	0.76	0.79	0.78	0.91	0.94	1.19	1.29	1.63
Height of last coil from the preceding	0.61	0.60	0.66	0.71	0.79	0.98	1.08	1.36
Width of last coil	0.95	0.98	0.96	1.04	1.08	1.16	1.21	1.40
Involution	0.15	0.19	0.12	0.20	0.15	0.21	0.21	0.27
Width of umbilicus . . .	0.68	0.65	0.75	0.81	0.83	0.80	1.00	1.06

	Constrictions cease; abdominal furrow becomes distinct; ribs cease to cross abdomen, and end in knots on the shoulders, they form bundles on the umbilicus, and bifurcate on the sides.				The central abdominal keel begins. The umbilical knots begin.		The sculpture becomes fainter. The two rows of shoulder knots subside into faint notches on almost continuous keels.	
	Metaneanic.					*Paraneanic.*		
	Cosmoceran.					*Hoplites.*		
	2⅜ coils.	2½ coils.	2¾ coils.	2 5/6 coils	3 coils.	3⅙ coils.	3 5/12 cls.	3½ coils.
	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
Diameter . . .	4.10	4.50	5.90	6.60	7.00	8.50	10.00	12.00
Height of last coil	1.83	2.00	2.80	3.15	. . . .	4.60	5.60	7.00
Height of last coil from the preceding . .	1.55	1.66	2.37	2.40	. . . . .	3.70	4.50	5.50
Width of last coil	1.70	1.71	1.85	2.07	. . . . .	2.55	3.00	3.60
Involution . . .	0.28	0.34	0.43	0.75	. . . . .	0.90	1.10	1.50
Width of umbilicus	1.16	1.32	1.40	1.46	. . . . .	1.58	1.70	2.00

	The septa begin to resemble *Placenticeras*.				The fine sickle-shaped ribs become suddenly coarse.		The notched keels give place to strong, elongated nodes ,and the central keel disappears.	
	Anephebic.				*Metephebic.*		*Parephebic.*	
	Transition from *Hoplites* to *Placenticeras*.				*Placenticeras.*			
	3¼ coils.	4 coils.	4¼ coils.	4½ coils.	4 5/6 coils	5⅙ coils.	5⅔ coils	6⅙ coils.
	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
Diameter . . .	15.00	20.50	26.50	34.50	47 00	67.00	118.00	172.00
Height of last coil	8.00	10.80	14.00	18.00	22.50	36.00	60.00	74.00
Height of last coil from the preceding . .	6.50	9.10	11.50	15.00	18.00	. . . . .	. . . . .	52 00
Width of last coil	4.00	5.00	6.75	7.75	12.00	19.00	25.00	35 00
Involution . . .	1.50	1.70	2.50	3.00	4.50	. . . . .	. . . .	22.00
Width of umbilicus	2.50	3.50	4.50	6.00	9.00	11.50	19.00	35.00

CONCLUSION AND SUMMARY OF RESULTS.

The development of *Placenticeras* shows that it is possible, in spite of dogmatic assertions to the contrary, to decipher the race history of an animal in its individual ontogeny. But the interpretation of ontogenic data is no simple problem of mere comparison of growth stages with antecedent genera; we must know the sources of error and apply the necessary corrections. We must guard against unequal acceleration, by which in the ontogeny of descendants characters are caused to occur together that belonged to different geologic generations of ancestors. An example of this is the central abdominal keel, that begins near the end of the cosmoceran stage, when no *Cosmoceras* nor even *Hoplites* ever had this; it is an adult character pushed back further than the other placenticeran characters by unequal acceleration. This inexact parallelism makes it impossible in many cases to correlate exactly a growth stage with the ancestral genus; otherwise it would be better to name the stage after the correlative genus, instead of using an arbitrary and artificial nomenclature such as has been adopted. When ontogenic stages are named after genera, it merely means that the characters of those genera are predominant.

Retardation plays an important part in the species discussed in this paper, showing itself especially in the septa, causing them to fail to reach the full development of *Hoplites*, the immediate ancestor of *Placenticeras*, and preventing individual ontogeny from giving the full ancestral record.

It is here demonstrated that new elements of the septa, contrary to the accepted belief, are sometimes added by subdivision of primary lobes on the outside, and not necessarily always in the part concealed by the involution, thus giving a reasonable explanation of the large number of small lobes found in such genera as *Beloceras*, *Pinacoceras*, and *Sphenodiscus*. The occurrence of lobes of this character does not show that such genera are related, but merely that each is a gerontic form, and that descendants of these are not to be expected in later formations. This does not apply to *Arcestes*, which has a large number of primary lobes, visible even on the second septum from the protoconch.

The stages wholly lost out of the ontogeny lie between the nautilian protoconch and the glyphioceran larval stage; this unrecorded part of the development is thought to have corresponded to the time spent in the egg. All later stages are recorded in ontogeny with a fair degree of distinctness.

The protoconch can not be correlated with any nautiloid, but the later stages can be compared with ammonoid genera, the exactness of the correlation becoming less as the stage advances, on account of unequal acceleration of development of ancestral characters, but on the other hand easier, on account of the greater number of characters one has to deal with.

The earliest larval stage is nautiloid in septa, but ammonoid in its calcareous protoconch. The middle larval stage is comparable with the Paleozoic group Glyphioceratidæ, probably *Glyphioceras* itself; the last larval stage is analogous to *Nannites*, a genus characteristic of the earliest Mesozoic.

In the adolescent period *Placenticeras* goes through at first a stage corresponding to *Cymbites*, or at least some *Cymbites*-like form, of the Upper Trias; then to some ægoceran genus of Upper Triassic or Lower Jurassic age; then to some one of the earlier perisphinctoid genera; then to *Cosmoceras* of the Jura, and lastly to *Hoplites* of the Cretaceous. It is thus demonstrated by ontogenic study that *Placenticeras* developed out of *Hoplites*, and thus belongs with that group near the Stephanoceratidæ, and not under the Amaltheidæ, with which it is classed in nearly all text-books. This relationship is shown also by the number of ammonite species intermediate in character between *Hoplites* and *Placenticeras*, although they are conventionally grouped under one or the other genus.

It is a mistake to class *Sphenodiscus* as a subgenus under *Placenticeras*, for it is neither ancestor nor descendant of that genus, but a parallel, independent development from the common stock *Hoplites*. The same retardation that caused the peculiar arrangement of the lobes in *Placenticeras* has gone even further towards simplifying the septa of *Sphenodiscus*, although this can not correctly, in either case, be ascribed to reversion, since while both fail to reach, in some respects, the full development of their ancestors, they do not return to the characters of any of their predecessors.

A parallel study of the ontogeny of two closely related species shows that the results must be interpreted with caution. *Placenticeras pacificum* and *P. californicum* certainly came from the same group of *Hoplites*, and probably from the same species, but in the late adolescent stage they are unlike, just as easily distinguishable as at maturity, owing to pushing back of specific characters into the adolescent period. Even in the *Cosmoceras* stage the two are quite distinct; the difference becomes less in the perisphinctoid stage, and undoubtedly the larval stages would be precisely alike in both. But this does not mean that the line of descent was the same only through the larval stages, and that the two species branched out from different perisphinctoid forms, for in all probability the perisphinctoid, cosmoceran, and *Hoplites* ancestors were the same for both species, and the differentiation could not have taken place before the Lower Cretaceous; the difference is due to unequal acceleration of characters.

The development of *Placenticeras* gives us an unusually fine illustration of the law of acceleration, or *tachygenesis*, with its two corollaries, unequal acceleration and retardation. In species from the Paleozoic or early Mesozoic we get better correlations of growth stages with ancestral genera, for with them there is little unequal acceleration, and almost no retardation apparent. But they are usually so poorly preserved that this sort of work is impossible with them. In Cretaceous species the preservation is usually better and the young specimens may be taken out from the old in good state of preservation, and the comparison with supposed ancestral genera facilitated. But in these later genera, so far removed in time from their origin, the development is so much more complex, on account of unequal acceleration, and in some cases on account of retardation, that correlation with ancestral genera is no longer a simple problem, although all the more fascinating because of its difficulty; it calls to its aid all the resources of biology and geology.

STANFORD UNIVERSITY,
CALIFORNIA,
March, 1900.

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EXPLANATION OF PLATE XXIV.

Placenticeras pacificum, sp. nov.

Figs. 1, 2. Protoconch from front and from above; 20 times enlarged. Arroyo del Vallé, Alameda County, California.

Fig. 3. Larval coil, diameter 1.16 mm., showing phylembryonic protoconch in the centre; 20 times enlarged. Arroyo del Vallé, Alameda County, California.

Figs. 4, 5. Transition from phylembryonic to ana- to meta-nepionic stages, diameter 0.76 mm., protoconch and one-third coil; 20 times enlarged. Arroyo del Vallé, Alameda County, California.

Figs. 6, 7. Protoconch and three-quarters of a coil, diameter 0.98 mm., beginning of the paranepionic stage; 20 times enlarged. Arroyo del Vallé, Alameda County, California.

Figs. 8, 9. Paranepionic, transition from glyphioceran to *Nannites*, one and one-twelfth coils; 20 times enlarged. Arroyo del Vallé, Alameda County, California.

Figs. 10, 11. Early adolescent (ananeanic), *Cymbites* stage, diameter 1.99 mm., one and seven-twelfths coils; 13 times enlarged. Henley, Siskiyou County, California.

Figs. 12, 13. Ananeanic, ægoceran stage, one and seven-eighths coils, diameter 2.64 mm.; 10 times enlarged. Arroyo del Vallé, Alameda County, California.

Figs. 14, 15. Ananeanic, perisphinctoid stage, diameter 3.50 mm., two and a quarter coils; 10 times enlarged. Arroyo del Vallé, Alameda County, California.

Figs. 16, 17. Metaneanic, transition from perisphinctoid to the cosmoceran stage, diameter 4.10 mm., two and three-eighths coils; 10 times enlarged. Arroyo del Vallé, Alameda County, California.

Figs. 18, 19. Metaneanic, cosmoceran stage, diameter 6.60 mm., two and three-quarters coils; 7 times enlarged. Arroyo del Vallé, Alameda County, California.

Figs. 20, 21. Beginning of paraneanic stage, transition from cosmoceran to the *Hoplites* stage, diameter 12 mm., three and a half coils; 2.7 times enlarged. Henley, Siskiyou County, California.

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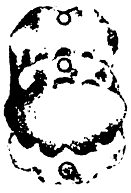
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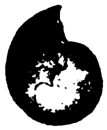
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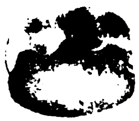
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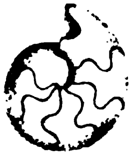
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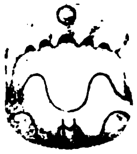
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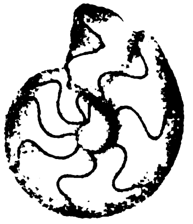
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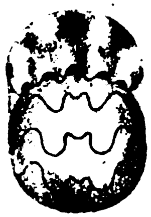
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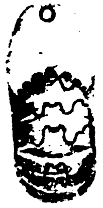
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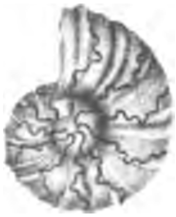
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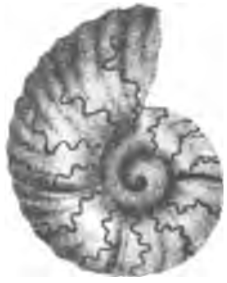
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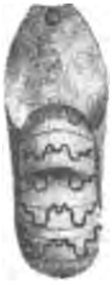
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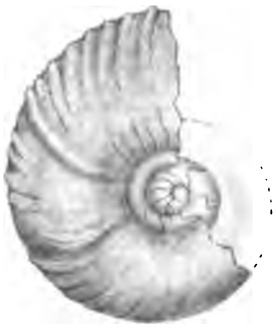
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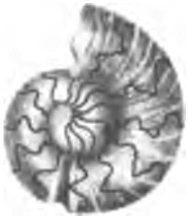
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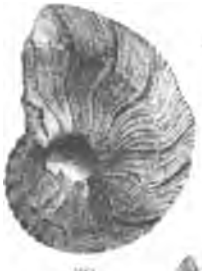
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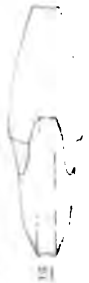
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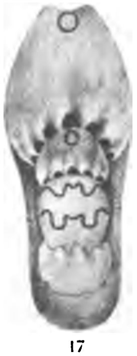
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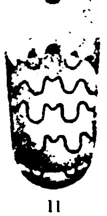
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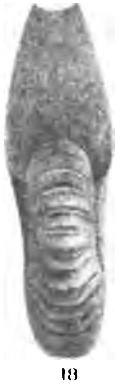
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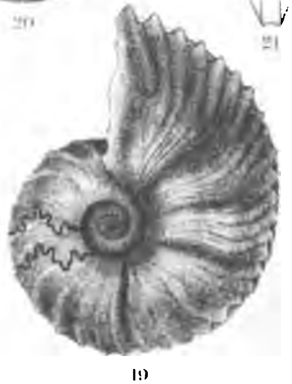
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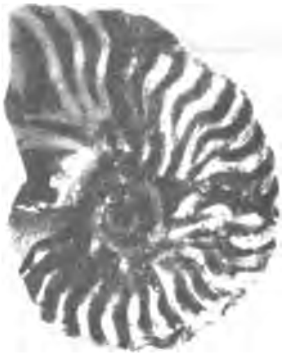
EXPLANATION OF PLATE XXV.

Figs. 1, 2.	*Placenticeras californicum*, adolescent, perisphinctoid stage, two and five-sixteenths coils, diameter 3.32 mm.; 10 times enlarged. Henley, California.
Fig. 3.	*P. californicum*, adolescent, transition from cosmoceran to the *Hoplites* stage; three coils, diameter 8 mm.; 2.7 times enlarged. Henley, California.
Figs. 4, 5.	*P. californicum*, adolescent, typical *Hoplites* stage, three and five-eighths coils, diameter 14 mm.; twice enlarged. Henley, California.
Figs. 6, 7.	*P. californicum*, adolescent, *Hoplites* stage, four coils, diameter 22 mm.; twice enlarged. Arroyo del Vallé, Alameda County, California.
Fig. 8.	*P. californicum*, transition from *Hoplites* to *Placenticeras*, four and a half coils, diameter 34.50 mm.; twice enlarged. Henley, California.
Figs. 9, 10.	*P. pacificum*, end of *Hoplites* stage, four coils, diameter 20.5 mm.; 2.7 times enlarged. Arroyo del Vallé, California.
Fig. 11.	*P. pacificum*, transition to *Placenticeras*, diameter 47 mm., four and five-sixths coils; natural size. Henley, California.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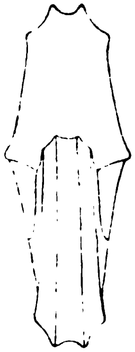
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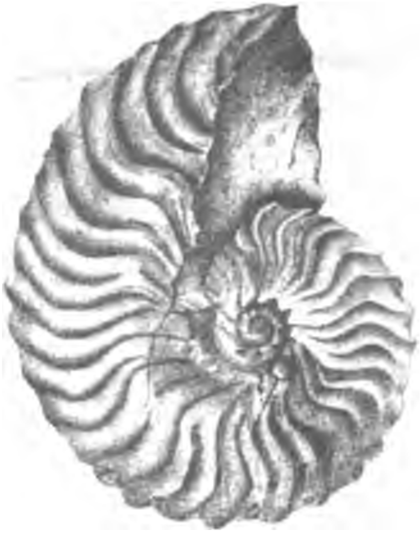
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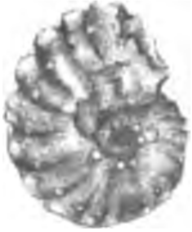
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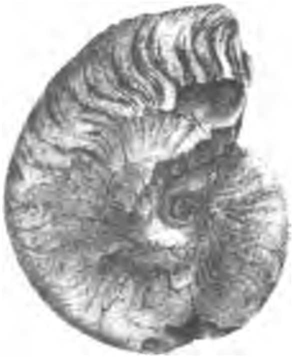
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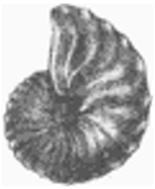
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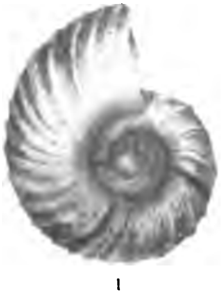
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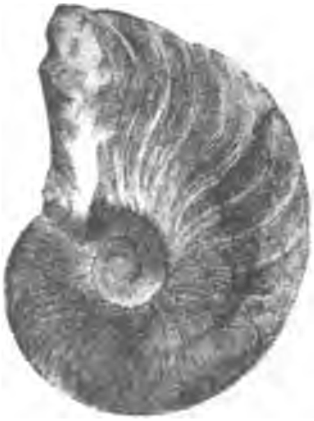
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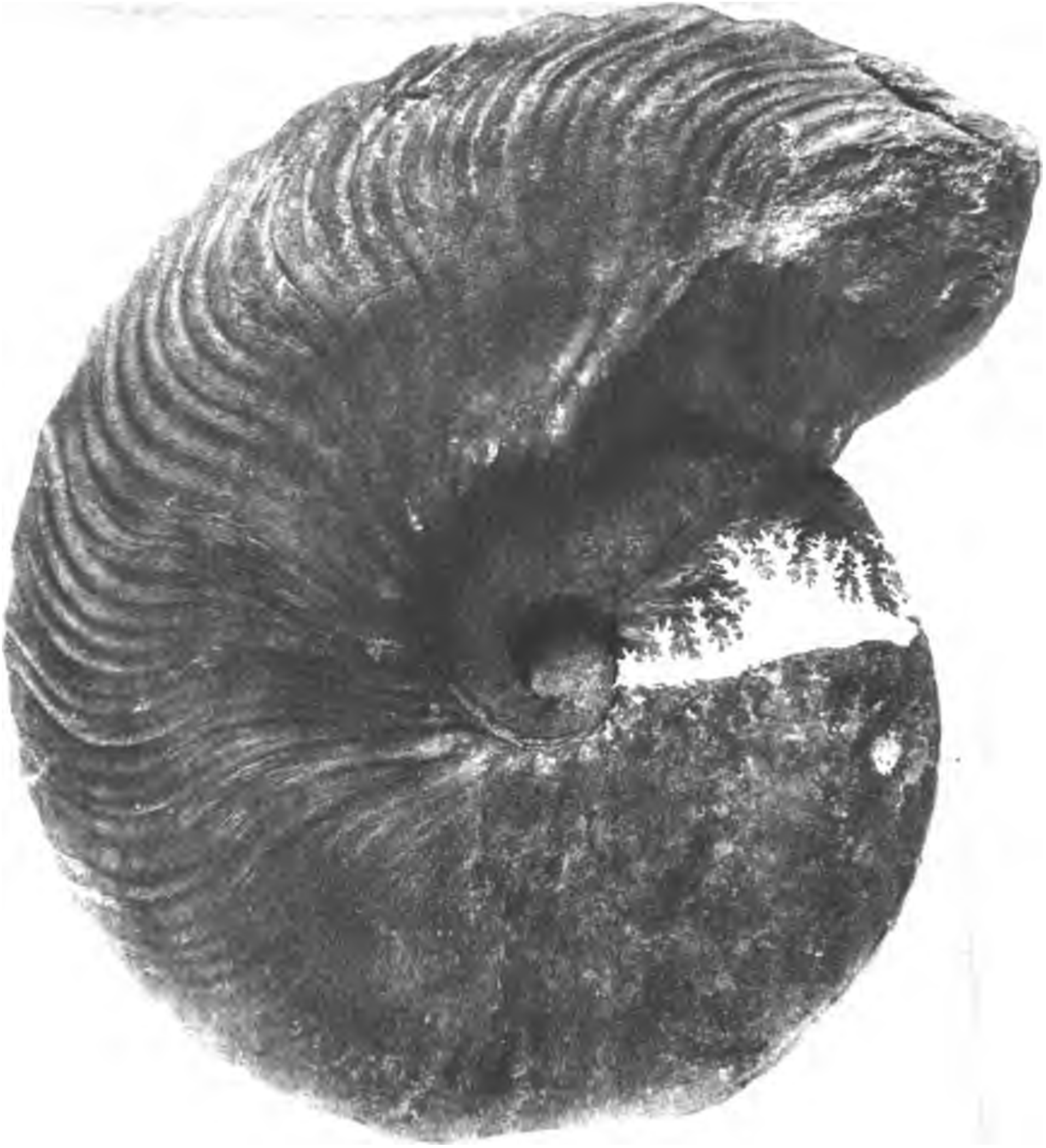
EXPLANATION OF PLATE XXVI.

(From a photograph by Franklin, Palo Alto, California.)

Placenticeras pacificum, sp. nov.

Adult shell, diameter 172 mm., six and a sixth coils, natural size. Henley, California. Type specimen, property of Frank M. Anderson, Yreka, California.



FRANKLIN, DEL.

PHOTO-LITH BRITTON & REY, S.F.

PLACENTICERAS PACIFICUM, SMITH.

EXPLANATION OF PLATE XXVII.

Development of the Septa of *Placenticeras pacificum*.

Fig. 1. First septum, ananepionic, nautiloid stage; 20/1.

Fig. 2. Septum at one-half coil, diameter 0.83 mm., metanepionic, glyphioceran stage; 20/1.

Fig. 3. Septum at one coil, diameter 1.16 mm., glyphioceran stage; 20/1.

Fig. 4. Septum at one and one-twe 1.32 mm., end of the paranepionic or end of larval stage, *Nannites* stage; 20/1.

Fig. 5. Septum at one and three-eighths coils, diameter 1.70 mm.; 20/1.

Fig. 6. Septum at one and five-eighths coils, diameter 2.20 mm., 20/1.

Fig. 7. Septum at one and three-quarters coils, diameter 2.40 mm., 20/1.

Fig. 8. Septum at one and seven-eighths coils, diameter 2.70 mm., transitional from Ægoceratidæ to the Perisphinctinæ; 20/1.

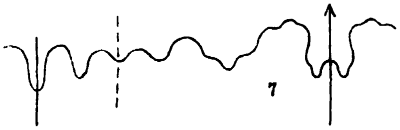
Fig. 9. Septum at two coils, diameter 3 mm.; 20/1.

Fig. 10. Septum at two and three-eighths coils, diameter 4.10 mm., *Cosmoceras* stage; 13/1.

Fig. 11. Septum at two and a half coils, diameter 4.50 mm., paraneanic, *Cosmoceras* stage; 14/1.

Fig. 12. Septum at two and seven-twelfths coils, diameter 5.50 mm., *Cosmoceras* stage; 14/1.

Fig. 13. Septum at two and three-quarters coils, diameter 6.25 mm., paraneanic, *Cosmoceras* stage; 14/1.



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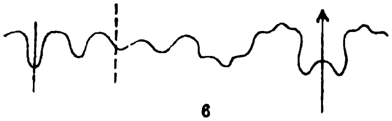

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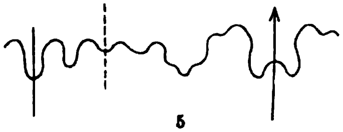

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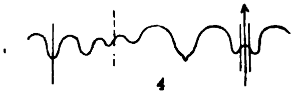

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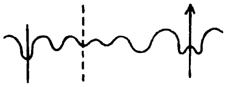

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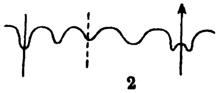

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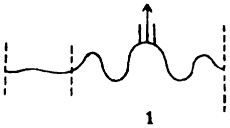

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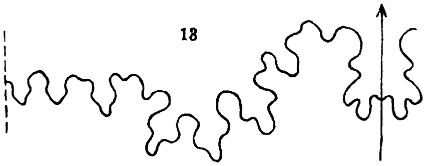

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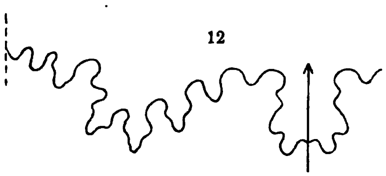

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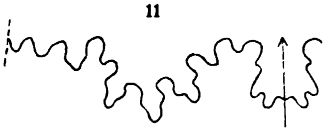

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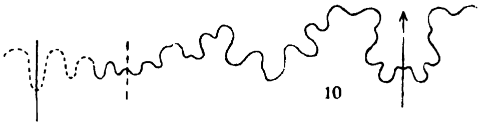

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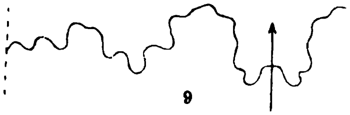

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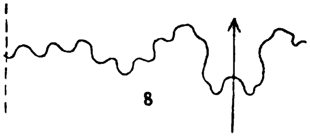

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PLACENTICERAS PACIFICUM.

EXPLANATION OF PLATE XXVIII.

Development of the Septa of *Placenticeras pacificum*.

Fig. 1. *Placenticeras pacificum*, septum at three and a sixth coils, diameter 8.50 mm., adolescent, about end of cosmoceran stage; 14/1.

Fig. 2. *P. pacificum*, septum at three and a half coils, diameter 12 mm., *Hoplites* stage; 14/1.

Fig. 3. *P. pacificum*, septum at three and three-quarters coils, diameter 14.50 mm.; the septa already show placenticeran characters, although the shell is still in the *Hoplites* stage; 9 times enlarged.

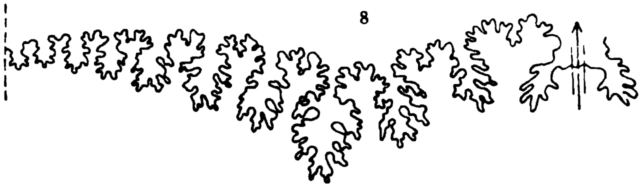
Fig. 4. *P. pacificum*, septum at maturity; natural size.

Fig. 5. *P. pacificum*, cross-section at four coils, adolescent, diameter 20.75 mm., showing inner whorls helmet-shaped, and the transition to the compressed, flat-sided placenticeran whorl; 4 times enlarged.

Fig. 6. Septum of *P. californicum*, adolescent, cosmoceran stage, two and three-quarters coils, diameter 4.70 mm.; 13 times enlarged.

Fig. 7. Early adult septum of *Diaphorites vetulonius* Fucini, for comparison. (After Fucini, *Pal. Ital.*, 1896, Vol. II, Pl. XXV, fig. 8.)

Fig. 8. Septum of *Placenticeras guadaloupæ* Roemer, for comparison. (After Roemer, Kreidebildungen von Texas, Pl. II, fig. 1.)



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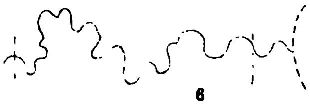

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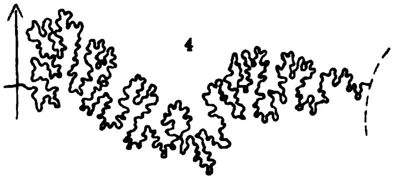

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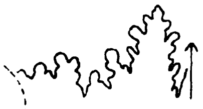

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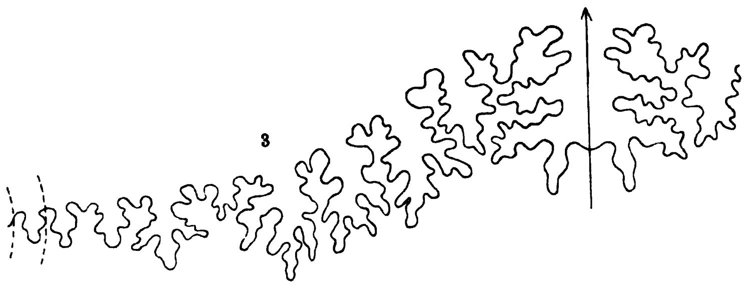

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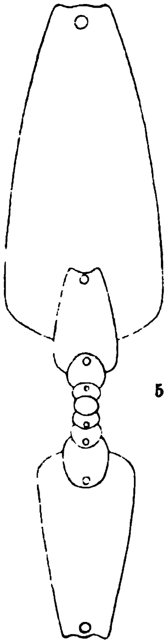

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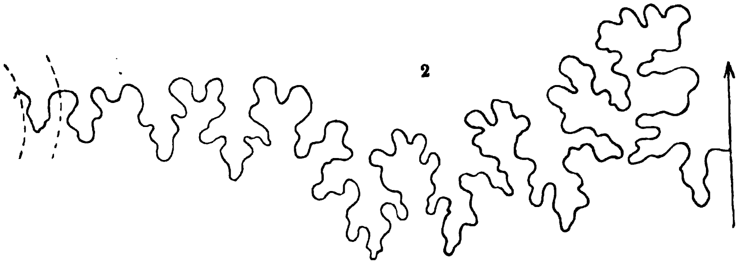

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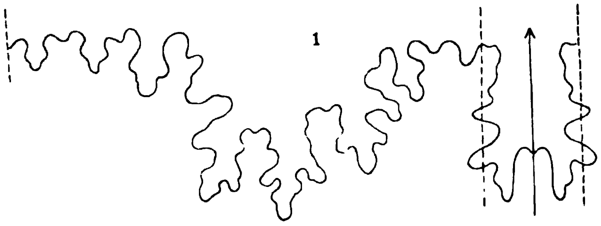

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Figs. 1-5 Placenticeras pacificum.
Fig. 6. Placenticeras californicum.

Fig. 7. Diaphorites vetulinus.
Fig. 8. Placenticeras guadalupæ.

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(Continued from Second Page of Cover.)

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